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THE ATTRACTION OF FREE-RANGING RAINBOW TROUT TO A FEEDING STATION

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A thesis submitted to the University of Stirling
for the degree of Doctor of Philosophy

August 1982

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7/83

ACKNOWLEDGMENTS

I particularly wish to thank Dr R.N. Gibson of the Scottish Marine Biological Association and Professor W.R.A. Muntz of Stirling University for their invaluable supervision during this study. I am also very grateful to Professor R.I. Currie for providing the facilities for this research at the Scottish Marine Biological Association's laboratory (Dunstaffnage Marine Research Laboratory) at Oban.

I would like to thank all the members of the S.M.B.A. who contributed to the study, but in particular I wish to thank Mr I.A. Ezzi for considerable assistance with many aspects of the work and Dr J.M. Graham for invaluable help with electronics.

Dr J.C.A. Craik of the S.M.B.A. kindly helped me with the identification of stomach contents, along with Dr W.J. Le Quesne (Homoptera), Mr C.A. Collingwood (Hymenoptera; Formicoidea), Dr M.R. Shaw (Hymenoptera; Parasitica), Dr V.H. Chambers (Hymenoptera), Mr D. Tozer (Coleoptera), Dr P.S. Cranston (Diptera; Nematocera), Mr E.A. Fonseca (Diptera), and Dr T.T. Macan (Plecoptera and Ephemeroptera).

I gratefully acknowledge the cooperation of Dr L. Ross and Dr M. Beveridge of the Institute of Aquaculture, University of Stirling with the work in Loch Fad. Dr L. Ross also provided invaluable help with the construction of the ultrasonic tags in the Biology Department at the University of Stirling. I also wish to thank Mr D. Sinclair and Mr J. Newton of the Department of Statistics, University of St Andrews for statistical advice and Dr A.D. Hawkins of the Marine Laboratory, Aberdeen, for advice, the loan of a J9 loudspeaker and help in constructing the sound spectrograms

I wish to thank Mr D.R. Kilpatrick for permission to, and considerable assistance with, work in Loch Charn. Mr T. Rae kindly allowed me to work in Loch Fad.

Special thanks are also due to Mrs C.A. Thomson and Mrs A. Harvey for the considerable time and effort they spent typing this thesis. Mr R.W. Summers kindly did the photographic work.

Finally, I would especially like to thank Sheila and my parents for their invaluable support.

Financial support was provided by a N.E.R.C. grant.

ABSTRACT

The aim of this work was to investigate techniques for controlling the movement of free-ranging rainbow trout. In the first part of the study groups of 50 rainbow trout were successfully conditioned to aggregate at a loudspeaker and feeding point in a 3.5 m x 3.5 m x 3.5 m enclosure in response to a pulsed 140-Hz sound signal played for 10 s prior to and during feeding. The development of the response was quantified using three techniques and a study of the factors involved in conditioning showed that, (1) the number of trials was the important criteria in establishing the conditioned response, (2) other fish and the visual cues associated with the experimental environment, as well as the sound signal, were used to mediate the conditioned response and (3) an increase in the size of the conditioning enclosure adversely affected the rate of conditioning.

Additional experiments showed that the sound signal amplitude was positively correlated with the number and activity of fish attracted to feed and that conditioned fish "generalized" to frequencies of between 50 and 380 Hz. Anaesthesia and handling, and 24 days without training, did not adversely affect the conditioned response.

In the second part of the study naive fish and fish pre-conditioned to a sound signal were released into an 8-acre loch in two separate experiments. These experiments examined the movements of rainbow trout in relation to an artificial feeding station and showed that fish were attracted to and remained close to the feeding station even in the absence of a sound signal. Pre-conditioned fish were not attracted to feed using sound although the experimental conditions prevailing at the time of this experiment could have adversely affected the results. A food delivery was, however, a very successful attractant and the possibility of feeding sounds being used in this attraction was investigated, but rejected. The role of other possible cues are discussed.

Further experiments quantified the diel changes in the number of fish and the size of the area covered by the group of fish at the feeding station and showed that ration size controlled the numbers aggregating there. The diet and return of stocked rainbow trout were analysed and compared with previous studies.

An additional study carried out in an 185-acre loch showed that a rainbow trout cage farm had a significant effect on the distribution of rainbow trout within the loch because the cages acted (unintentionally) as supplementary feeding points. Their behaviour is discussed in relation to the results from the previous experiments.

Some observations on the swimming behaviour of rainbow trout in sea cages are also discussed.

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SECTION 1

GENERAL INTRODUCTION

The main aim of this study was to evaluate the feasibility of farming rainbow trout, Salmo gairdneri Richardson, in a large body of water and to investigate methods of controlling their movements for feeding and harvesting.

Earlier work has shown that rainbow trout may be reared in productive fishless lakes, both in Canada (Bernard and Holmstrom, 1978) and the USSR (Arendarenko and Zabolotskiy, 1977). Similar extensive farming enterprises are also an attractive proposition in the United Kingdom, because the overheads could be less than those associated with the feeding and tanks or cages of more conventional fish farming practices. More efficient use could also be made of available water resources (Landless, 1978). In Scotland, in particular, there are a large number of waters which could be managed to produce more fish but, although with the correct stocking and cropping policies some improved harvest may be attained, in many of the less productive waters supplementary feeding would be required to maintain viable growth rates and stocking densities. This necessity to feed is predictable from the known population dynamics of natural lacustrine salmonid populations where growth on a natural food supply on a given water is usually negatively correlated with population density (Campbell, 1971; Jensen, 1977).

Mason (1974) has shown that supplementary feeding of juvenile coho salmon, Oncoryhnchus kisutch, in a stream resulted in less emigration, increased survival and biomass and an increase in lipid reserves compared to unfed stream controls. Supplementary feeding could, therefore, be used to increase the production from a stream and indeed this principle has more recently been applied to the high density culture of coho salmon smolts in stream channels where fish are grown on a diet of both natural and artificial food (Mundie and Mounce, 1978; Mundie, 1980). Novotny (1980) and Ritter and Carey (1980) have also suggested that coho and Atlantic salmon may be reared extensively in lakes using supplementary feeding.

The disadvantages of any lake rearing programme are that supplementary feeding and harvesting are potentially more difficult than conventional farming, thus reducing the return of stocked fish and offsetting, to an unknown degree, the reduction in overhead costs. Therefore, although fish might be attracted to shelter and sites of particularly abundant food resources (Wilbur, 1974, 1978; Wilbur and Crumpton, 1974; Fishelson, 1980), it is intuitively desirable to have a more precise means of controlling fish behaviour.

Balchen (1977a) and Bardach and Magnuson (1980) describe some potentially useful stimuli for controlling fish behaviour. Acoustic stimuli are potentially one of the most useful (Balchen, 1977a) because they are easily generated, propagate rapidly, may provide directional information over relatively large distances and are independent of variations in light intensity, although, as Tavolga (1980) points out, their potential has never been realised.

Many attempts have been made to attract or repel fish using artificially generated sound stimuli. Among early experimenters, Zenneck (1903, in Protasov, 1965) and Bigelow (1904) both noted an increase in locomotor activity in the presence of sound. Attempts to obtain consistent avoidance responses, however, have generally failed (Moulton and Backus, 1955). For example, Shishkova (1958, in Protasov, 1965) attempted to frighten mullet into a stationary seine net using 10 -10,000 Hz stimuli but failed because the fish reacted to the noise by diving to the bottom and not horizontally into the net. Protasov (1965) considered that this diving behaviour was a natural fright reaction for this species, thus illustrating the importance of using relevant sounds in the correct behavioural context. More recently, Chapman (1976) recorded consistent avoidance responses in a natural gadoid population to low frequency (f < 160 Hz) narrow band noise although the fish habituated relatively quickly to these stimuli. Such avoidance, followed by habituation,appears to be the typical unconditioned reponse to most artificial sound stimuli (Moulton, 1964) although there is some interspecific variation in this response (Malyukina, 1960, in Protasov, 1965). For example, gadoids are known to habituate more quickly to artificially produced stimuli than clupeoids (Balchen, 1977a) and fish usually habituate quicker to pure tones than more erratic stimuli. In fact, Balchen (1977a,b) suggests that because of the relative sensitivity of clupeoids they may be successfully steered using avoidance responses.

Several attempts have also been made to attract or repel salmonids using acoustic stimuli with the original impetus for this research coming from attempts to guide young migrating salmonids away from hydro-electric dam intakes. Burner and Moore (1953, 1962) tried a variety of devices, with frequency responses ranging from 67 Hz to 70 kHz, in an attempt to elicit any useful responses from rainbow trout, Salmo gairdneri, and brown trout, Salmo trutta. In addition, Kerr (1953), Brett and MacKinnon (1953), Moore and Newman (1956), Brett and Alderdice (1958) and Vanderwalker (1967) have carried out similar experiments. The results of all this research have shown that, even with very high amplitudes, a startle reaction followed by rapid habituation is the characteristic response to low frequency sounds and that high frequencies have no effect. These results are in accordance with the work of Hawkins and Johnstone (1978) who found that the Atlantic salmon, Salmo salar, had an upper frequency limit of around 380 Hz. This value was determined in the sea, away from the surface and other reflective boundaries, although in tanks, where very high particle displacement amplitudes can be generated for a given sound pressure, the upper frequency limit may extend upwards to 580 Hz (Hawkins and Johnstone, 1978).

To be attractive a sound must have some biological relevence. For example, Tavolga (1958) found that the courtship sounds of male Bathygobius soporator elicited an approach response in other males and an increase in the activity of females. Chapman (1976) found that a wild gadoid population in Loch Torridon were attracted to pure tone stimuli of between 30 and 110 Hz although pulsed stimuli in this frequency range were thought to be even more effective. Again, higher frequencies had no effect. Chapman (1976) considered that the success of this attraction was due to the fact that low frequency sounds were important in the feeding behaviour of these fish. In fact, noises imitative of food items or other feeding fish have been most successfully used as attractants and low frequency and irregular pulsing are usually the most common denominators of these stimuli.

The importance of producing erratic, low frequency stimuli and their relevance to feeding behaviour has been emphasized in the extensive work on the acoustic behaviour of sharks (summarized by Myrberg, 1978). These studies have shown that only broad band, low frequency stimuli, less than 800 Hz, are attractive and that irregular pulsing is an essential component of any attractive stimulus. These stimulus characteristics correspond with some of the noises of the shark's prey, as Banner (1972) demonstrated that in the lemon shark (Negaprion brevirostris) the relative attractiveness of a sound is correlated with its similarity to the sounds produced by other fish.

Several teleost predators (and significantly, no herbivores) were also attracted during some shark studies (Steinberg et al., 1965; Nelson et al., 1969), and again the lower frequency sounds of an "impulsive" nature were the most effective attractants because they were thought to simulate certain aspects of their prey's behaviour (Richard, 1968). Such biologically significant sounds may be used to enhance fishing success and Westenberg (1952) and Moulton (1964) provide several interesting examples of instruments, such as the "cotio-cotio" and "xoyo", used in some primitive fisheries whose success supposedly lies in their imitation of feeding sounds. Similarly, the playback of sounds associated with feeding have been used more recently to improve fishing success in some Japanese fisheries (Hashimoto and Maniwa, 1967, 1971; Maniwa et al., 1973; Maniwa, 1976).

There is little evidence that salmonids, primarily visual feeders (Ali, 1959; Protasov, 1968; Ware, 1973; Wankowski, 1977), may be attracted by acoustic stimuli although Maniwa et al. (1973) mention that "swimming and bait eating" sounds of pink salmon (Oncorhynchus gorbuscha) were successfully used to increase catches in a stationary net. An originally neutral stimulus may, however, acquire a biological significance through conditioning. For example, Chapman et al. (1974) found that a local population of Gadus morhua, Pollachius virens, P. pollachius and Limanda limanda in Loch Torridon became conditioned to the noise of divers' demand valves, learning to associate these sounds with food disturbed during diving. Nelson and Johnson (1976) also present some anecdotal evidence that sharks may become conditioned to the sound of a spear gun and Margetts and Bridger (1971, in Chapman, 1976) and Caddy (1973) noticed aggregations of fish in trawl tracks that may have been attracted through conditioning to the low frequency vibrations associated with trawling (Chapman, 1976).

In a large sea enclosure in Norway, Olsen (1976) and Balchen (1977a,b,c) conditioned saithe, Pollachius virens, to move between feeding stations, each comprising a loudspeaker and a feeding point, in response to a sound signal and in anticipation of feeding. Both authors suggested that a series of such feding stations could be used to lead saithe, which were stored in enclosures, to a harvesting point. Abbott (1972) similarly conditioned 13,000 rainbow trout to aggregate at a loudspeaker in a 0.25 acre pond in response to an 150 Hz tone played for 1 min before feeding. Thus, the application of conditioning techniques shows some promise for a precise control of fish behaviour and the main aim of the present study was to investigate how they may be applied to control the movements of rainbow trout. The study was therefore divided into two main sections; the first examined the conditioning of rainbow trout to sound in an enclosed environment and the second investigated the response of free-swimming fish to sound and feeding points in a large body of water.

SECTION 2

THE CONDITIONING OF RAINBOW TROUT TO A SOUND SIGNAL

2.1. INTRODUCTION

McDonald (1921), Westerfield (1921), Von Frisch (1923) and Bull (1928) were among the earlier workers who succeeded in conditioning fish to a sound stimulus using food as a reward. Moorhouse (1933) conditioned surf perch, Cymatogaster aggregatus, to a horn in a small tank with the operant response being an aggregation around the feeding point in response to the sound alone. More recently, Fujiya et al. (1977), working in a 4m diameter tank, conditioned 800 red sea bream, Pagrus major, to aggregate at a feeding point in response to a 200 Hz tone. Eastcott (1978) also conditioned carp (Cyprinus carpio) and thick-lipped mullet (Crenimugil labrosus) to obtain food by pressing a trigger in response to a 250 Hz pure tone. Similar appetitive conditioning techniques have been widely used in auditory research (e.g. Poggendorf, 1952; Protasov, 1965; Schuijf et al., 1972; Schuijf and Buwalda, 1975).

Several authors have conditioned salmonid species to acoustic stimuli. For example, Facey et al. (1977) and Hawkins and Johnstone (1978) classically conditioned heart rate bradycardia in Atlantic salmon, Salmo salar, using pure tone acoustic stimuli as the conditioned stimulus and an electric shock as the unconditioned stimulus. Stober (1969) also classically conditioned bradycardia in cutthroat trout, Salmo clarki, using light as the unconditioned stimulus. Healey (1967) and Larson and Donaldson (1969) have also conditioned pink salmon, Oncorhynchus gorbuscha and rainbow trout, Salmo gairdneri, respectively to aggregate at a feeding point in response to a sound signal in a small tank. However, the complex acoustic environment in a tank bounded by air (Parvalescu, 1967) makes it difficult to extrapolate the responses observed under these conditions to the field and thus it is desirable to carry out experiments relevant to the field actually in the field. The present experiments, which were used to gain background information for use in the field, were therefore carried out in large nets in the sea.

In a large sea enclosure in Norway, Olsen (1976) and Balchen (1977 a,b,c) succeeded in conditioning saithe (Pollachius virens) to move between loudspeaker/feeding points in response to a variable frequency sound signal. Fujiya et al. (1980) found that preconditioned red sea bream, Pagrus major, aggregated close to a similar feeding station in the sea, although in this case it is not clear whether the fish were responding to the sound signal or the regular addition of food. Abbott (1972) showed that rainbow trout in a 0.25 acre pond could be conditioned to gather around a loudspeaker in response to an 150 Hz pure tone played for 1 min prior to the delivery of food by an unconcealed observer. Qualitative analysis suggested that conditioning was complete after 45 trials when approximately 70 to 90% of the fish in the pond were seen to aggregate close to the loudspeaker in response to the tone. Similarly, Landless (1976a) conditioned rainbow trout in sea cages to show a "feeding response" to an 100 Hz tone played for 30 s prior to a food delivery.

Although the above results suggest that rainbow trout may be conditioned to aggregate at a feeding point in response to a sound stimulus, no experiments have examined the development of these conditioned responses in any quantitative manner and there is no information on the relative importance of acoustic and other cues in mediating the responses. The present section therefore describes how rainbow trout were conditioned to aggregate at a feeding station in enclosures in the sea. Particular attention was paid to the relationship between the number of trials required and the time over which these were spread, the effect of different sized enclosures on the rate of conditioning and the cues used by rainbow trout to mediate their conditioned response.

2.2. MATERIALS AND METHODS

2.2.1. Experimental animals and holding facilities

Rainbow trout, Salmo gairdneri, of approximately 50g were purchased from the freshwater sites of either Comrie Fish Farm or Kames Fish Farming Ltd. and transferred directly to the sea cages in Dunstaffnage Bay, adjacent to the Scottish Marine Biological Association's laboratory near Oban. Further details of the transfer procedure and holding facilities are given in Landless (1974a, 1976b) and Jackson (1979).

Previous exposure to the conditioned stimulus may influence future learning (Mackintosh, 1974). To prevent experimental fish from gaining any experience of the experimental sounds fish were therefore transferred to and held in similar cages in Saulmore Bay, one mile east of Dunstaffnage Bay, prior to the start of any acoustic work.

Fish may learn to become active prior to feeding time if a fixed feeding regime is used (Davis and Bardach, 1965). The timing of food aquisition tasks in relation to this conditioned activity peak may influence the learning rate of that task (in chickens; Reymond and Rogers, 1981). Fish were therefore hand fed once or twice a day at an irregular time in Dunstaffnage Bay and then by an automatic feeder (Tess Aquaculture Ltd.) programmed to deliver food every forty minutes during daylight hours in Saulmore Bay. Fish were fed floating food (Mainstream Expanded Trout Pellets, B.P. Nutrition or Omega Trout Food, Floating Type, Edward Baker Ltd.) delivered according to manufacturers daily specifications at different temperatures (recorded at a depth of 1 m) (Appendix E).

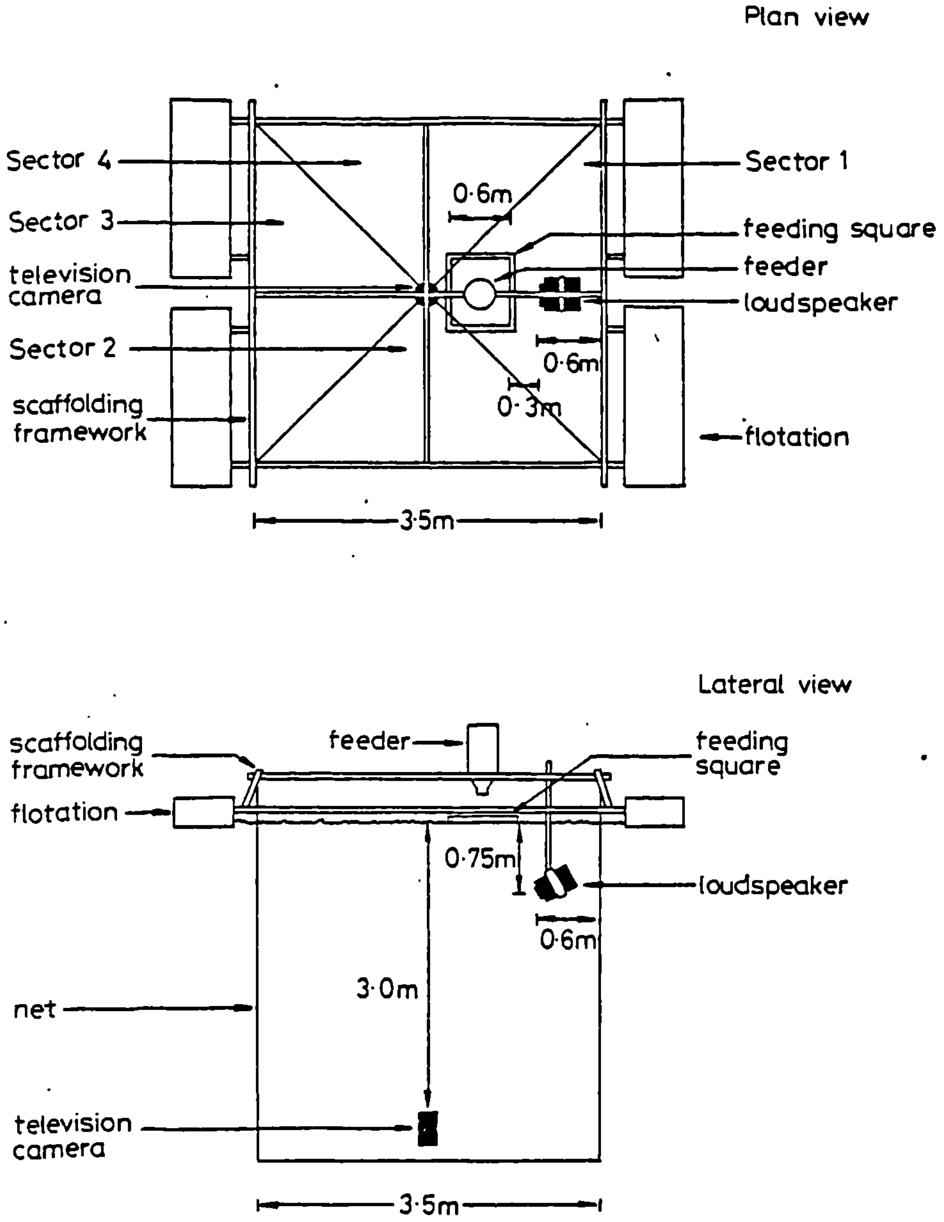


Figure 2.1. Diagrams of the experimental cage used during Conditioning Experiments 1 - 4.

2.2.2. Instrumentation

An underwater television camera (Nuvicon camera; Chalnicon tube; Marine Unit Technology;) was used to observe fish behaviour. The camera was mounted in the centre of the cage pointing vertically upwards from a depth of 3m on a scaffolding frame which was bolted to the cage superstructure (Figure 2.1). In this position the camera collected debris and therefore required regular in situ cleaning to maintain the picture quality. To protect the end window of the camera from damage and to improve picture quality during bright sunshine a neutral density filter was placed over the end window. The video signal from the camera was recorded on a National Panasonic portable video recorder (Model NV 3085-E), at 50 frames.s^{-1}, using Sony high density video tape. The image could be viewed simultaneously or later using a portable video monitor (National Panasonic; Model WV 5310 E/B). This equipment was housed in a hut on the sea cages and powered by batteries which could be switched on remotely, using relays, via cable connections to the laboratory, approximately 250 m away (Figure 2.2).

The recorded tapes were returned to the laboratory for playback on the portable video recorder or a time lapse video tape recorder (National Time Lapse VTR, Model NV-8030) and a mains operated monitor (Electrohome Ltd.) For analysis, a digital displayed time base was added to the video picture by re-recording the video tape after passing the signal through a video-timer (For-A Company Ltd; Video Timer Model VTG 33).

During analysis the video picture was replayed and displayed on the mains operated monitor with a reduced screen size to help preserve the geometry of the field of view. To investigate the distortion of this field of view a grid composed of 2cm x 2cm squares was observed at a 10cm distance from the camera underwater in the laboratory. The dimensions of the picture displayed on the monitor were 20 cm x 16 cm and there was no visible distortion within a

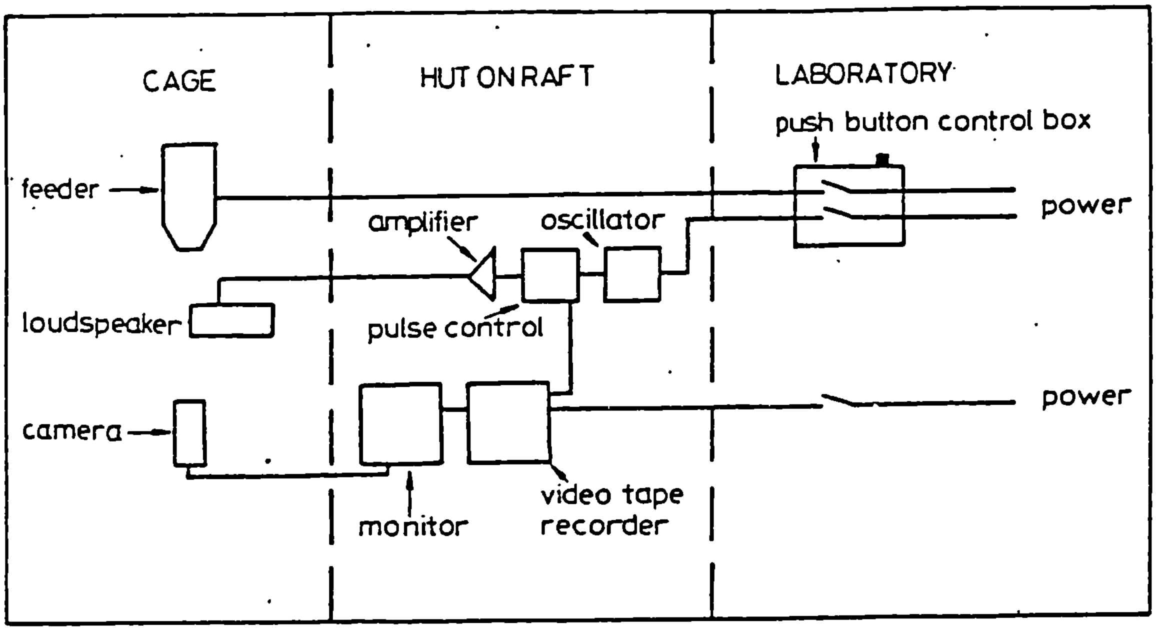


Figure 2.2. Block diagram of the apparatus used during the conditioning experiments.

18 cm x 13.5 cm central rectangle. With the camera in position in the cage the surface area of the net filled a central 16cm x 16cm square, so there was a slight distortion of the periphery of the vertical axis of the field of view. This distortion corresponded mostly with Sectors 2 and 4 which were not considered during the majority of the later analysis (Section 2.3).

Sound stimuli were generated by an 140 Hz oscillator which fed a power amplifier designed and built at the S.M.B.A. by Mr. R. Bowers. The amplifier then fed an underwater loudspeaker. The signal level was determined using an oscilloscope as the maximum possible output without any visible distortion of the sine wave. An oscillator control box was designed and contructed by Dr. J. Graham to pulse the output of the oscillator at a rate of 2 s on and 0.5 s off. To stop transient noises occuring as the oscillator warmed up there was a delay of 5 s between the power to the amplifier being switched on and the oscillator being switched in. Although no transients resulted from the electronics the fast rise and fall time of the sound signal gave rise to slight transients when the pulse came on and off due to the slower response time of the loudspeaker.

To generate sounds in water, moving coil sound projectors were employed (Dyna-Empire type J9 or Marine Resources Inc. type J9). As two loudspeakers were not simultaneously available a dummy loudspeaker was employed for some experiments. The dummy was constructed from plastic and both it and the live loudspeaker were inserted inside a thoroughly wetted (to remove air bubbles) black polythene cover during experiments. A cable was also added to the dummy so that both were visually identical in the water. The polythene had no measurable effect on the sound pressure level of the signal from the loudspeaker and so, to ensure that visual cues remained constant throughout all the experiments, the cover was continually kept on. This eliminated fouling of the actual loudspeaker during immersion periods of up to 3 weeks.

During experiments fish were fed using laboratory made feeders containing an electrically driven worm screw. The feeder was calibrated by weighing the food delivered with the feeder on for known time intervals. The amount fed could be described by the regression equation:

$F = 5.843 + 37.864\,T$

F = amount fed (g); T = motor on time (s)

$t = 66.53$; d.f. = 38 ; $p < 0.001$

The variability of the actual deliveries used during the experiments is shown in Table 2.1.

The feeder delivered food into the centre of a floating feeding square (60 cm x 60 cm internal dimensions) made from 6cm diameter PVC tubing filled with polystyrene foam. This structure served to limit the distribution of the floating food.

A block diagram of the apparatus used is shown in Figure 2.2.

2.2.3. Measurement of sound stimuli and ambient noise.

The sound stimuli were monitored by either one of two calibrated hydrophones sensitive to sound pressure (Plessey MS83 or Celesco Transducer Products Inc. LC10). The signal from the hydrophone fed either a built-in pre-amplifier in the Plessey hydrophone or another pre-amplifier (Celesco Transducer Products Inc. LC 1300) connected 15.2 m away from the Celesco hydrophone. The signal level was then measured with a calibrated precision sound level meter (Bruel and Kjaer, type 2203). Sound pressure level was expressed in decibels relative to a sound pressure of 1 microbar, i.e. dB//1µbar where 1µbar = 0.1 Newton. m^{-2}.

The above equipment was also used to measure the ambient noise but, in addition, the signal fed an octave filter set (Bruel and Kjaer, type 1613) with the centre frequencies of interest ranging from 31.5 to 1000 Hz. Because such measurement entails using variable width filters, ambient noise was expressed in terms of the sound spectrum level. This is the sound pressure level in a frequency band 1 Hz wide and can be calculated using the following equation from Urick (1975):

$$S.L. = B.L. - 10\log F$$

S.L. = spectrum level (dB// 1μbar. Hz^{-1})

B.L. = broad band level (dB//1 μbar)

F = filter band width (Hz).

2.2.4. Pre-experimental procedure

Experiments were carried out in Dunstaffnage Bay. Prior to each experiment approximately 100 fish were transported by boat from Saulmore to Dunstaffnage Bay in 90-l dustbins containing oxygenated water. Fish were then anaesthetized in a benzocaine solution ($25mgl^{-1}$) (Taylor and Solomon, 1979) in sea water and 50 fish of a similar length were measured (total and fork length, nearest mm) and weighed to the nearest 5 g using a spring balance. These fish were then introduced into the experimental net and allowed to recover for at least 4 days prior to the experiment.

The temperature was recorded at a depth of 1m prior to each experiment and these measurements together with the total weight of the fish were used to calculate the ration level for each experiment. This level was set according to the food manufacturers specification (Edward Baker Feeding Guide; Appendix E). Details of the fish stocks and rations used are given in Table 2.1. The ration was fed over the pre-experimental period and the experiment commenced when it was consumed in a single 15-min feeding session. Food was randomly distributed over the cage during this period in order to stop fish associating any particular area of the cage with food.

Table 2.1. Details of the conditioning experiments and the rainbow trout used during these experiments. The mean temperature refers to the mean pre-trial value which was used to calculate the ration. The temperature range refers to the values encountered during the experiment.

Experiment Number	Trials per day	Temperature (°C) $\bar{X}\pm$ range	Number of fish used per experiment	Fork length(mm) $\bar{X}\pm 1$ s.d.	Weight(g) $\bar{X}\pm 1$ s.d.	Ration fed per day (% total body weight)	Ration fed per day(g) ±95% confidence limits
1	6	12.0 (12.0-13.0)	50	222 (±12)	125 (±28)	1.6	100 (±25)
2	6	13.0 (13.0)	50	232 (±12)	206 (±32)	1.6	165 (±27)
3	3	12.5 (10.0-12.5)	50	243 (±16)	205 (±36)	1.55	159 (±26)
4	6	9.0 (8.0-9.0)	50	263 (±12)	243 (±38)	1.1	134 (±25)
5	6	10.5 (10.0-13.0)	50	208 (±13)	124 (±11)	1.45	90 (±25)
6	6	14.0 (13.0-14.0)	203	238 (±20)	183 (±49)	1.75	650 (±29)

2.2.5. Experimental procedure

2.2.5.1. Conditioning experiments in the small net

The first set of experiments (Expts 1,2,3 and 4; Table 2.1) were carried out in a 3.5m x 3.5m x 3.5m net (Figure 2.1). The loudspeaker was deployed at a depth of 0.75 m and held at an angle of 30° to the horizontal by a bracket attached to the cage superstructure. To minimize transmission of vibrations to the cage, 12mm thick padding surrounded the loadspeaker where the bracket was attached. The loudspeaker was placed relatively close to the feeding point as a close association of the two may facilitate learning (Sutherland, 1961; Muntz, 1974). Trials followed the classical conditioning paradigm of delayed conditioning (Mackintosh, 1974) and consisted of a 10-s pulsed (2 s on: 0.5 s off) 140-Hz sound signal played prior to and during feeding. An 140-Hz signal was chosen because salmonids are most sensitive to pure tones around this frequency (Hawkins and Johnstone, 1978). A profile of the sound pressure levels recorded in the experimental cage is shown in the results section (Section 2.3.3; Figure 2.27). The sequence of events was initiated in the laboratory by a push button electronic timing device (Appendix C) connected to the raft via submerged cables (Figure 2.2). By pushing the button the operator initiated a programmable and accurate sequence which first, switched on a relay to provide power to the oscillator, amplifier and loudspeaker and secondly switched on a relay to provide power to the feeder. Both relays were switched off simultaneously.

Trials were carried out at regular times throughout the day. Three experiments (Expts 1,2 and 4) were carried out with 6 trials per day (0930; 1054; 1218; 1342; 1506; 1630) and one (Expt 3) at three trials per day (0930; 1300; 1630). Details of the fish used in these experiments are shown in Table 2.1.

Samples of fish behaviour were recorded using the television camera and video tape recorder before, during and after each trial. These commenced

5 min prior to each trial with 15-s recordings taken 5 s before and 10 s after every minute. From 1 min prior to the trial the video tape recorder remained on until 1 min after. The camera remained on throughout all of the 6 min sampling period. All this sampling procedure was carried out from the laboratory via the cable connections to the raft to prevent disturbance of the fish.

2.2.5.2. Conditioning experiments in the long net

The second series of experiments (Expts 5,6;Table 2.1) involved a 17 m x 3.5 m x 3.5 m net stretched beneath four adjoining cages. The feeder and feeding ring were placed in the centre of one of the end cages with the loudspeaker 15 cm to one side of the ring suspended horizontally on ropes at 1.5 m depth pointing towards the main body of the cage. The greater depth was chosen because the sound stimulus propagates better from this depth than at 0.75 m. (Section 2.3.3). In order that the results of these experiments would be comparable with those in the smaller net the sequence of events and samples taken during each trial were identical to those described previously in Section 2.2.5.1.

2.3. RESULTS

2.3.1. Conditioning experiments in the small net

2.3.1.1. General results

The unconditioned response to the sound stimulus was a startle reaction away from the sound source by fish near to the source which usually increased the general activity of the rest of the group. No natural attraction to the source was observed. The conditioned response to the conditioned stimulus was a consistently tight aggregation around the area of the loudspeaker (Figure 2.3).

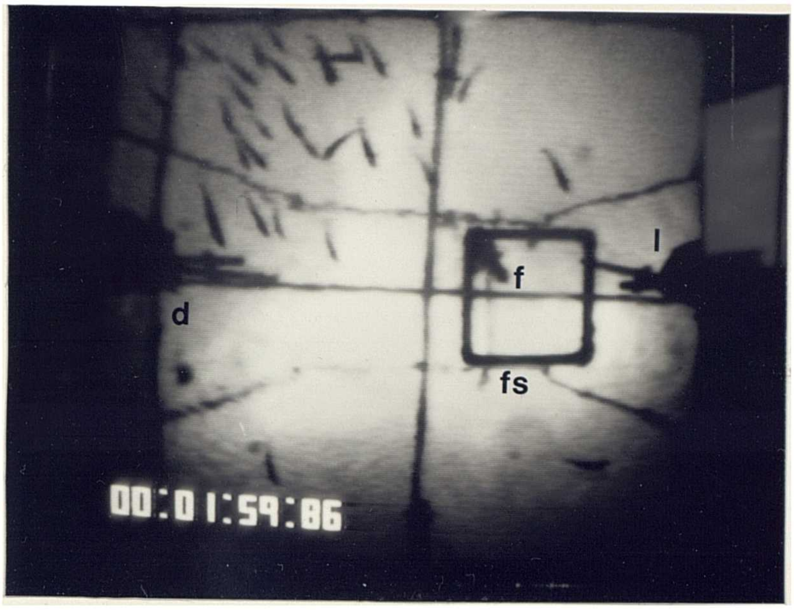
Figure 2.3. Photographs taken from a video tape of a well conditioned response.

(a) shows the behaviour immediately pre-trial.

(b) shows the behaviour at the end of Pulse 4 of the conditioned stimulus.

(c) shows the fish feeding.

The photographs also show the "live" loudspeaker (l), the "dummy" loudspeaker (d), the feeder (f) and the feeding square (fs).



a

b

c

Each experiment, except Experiment 1, was continued until there were ten such consecutive responses.

2.3.1.2. Development of the conditioned response : aggregation around the feeding station

2.3.1.2.1. Introduction and methods

For the purpose of analysis the video monitor was divided into 4 sectors (Figure 2.1). The number of fish in the sector containing the feeder, feeding square and loudspeaker (Sector 1) was counted at 1 min intervals starting 5 min prior to each trial. Subsequent counts were initially made at 1-s intervals throughout the conditioned stimulus although after preliminary analysis they were made only at the end of the 4th pulse (9.5 s after the start of the conditioned stimulus). The total number of fish observed feeding was also counted.

Some errors were involved with the above method as it was not possible to see fish if they moved close to the edge of the cage as a result of the dark background of the net. In rough weather the cage, and as a result the camera, moved around slightly so the fish were not always in the same position relative to the cage even though they may have been stationary. In bright sunlight the contrast was too great for a clear silhouette of all the fish and so those in front of the sun were not visible. The sun never encroached on the feeding area, however, so reasonable visibility was maintained in this area on most trials. Fish moving very close to one another were sometimes difficult to distinguish individually and those entering the feeding area from darkened areas of the cage were also difficult to see although most fish converged on the feeding area from the front, and if separate they were easy to count. In order to compare experiments carried out under varied environmental conditions, however, the number counted in each sector was expressed as a percentage of the total

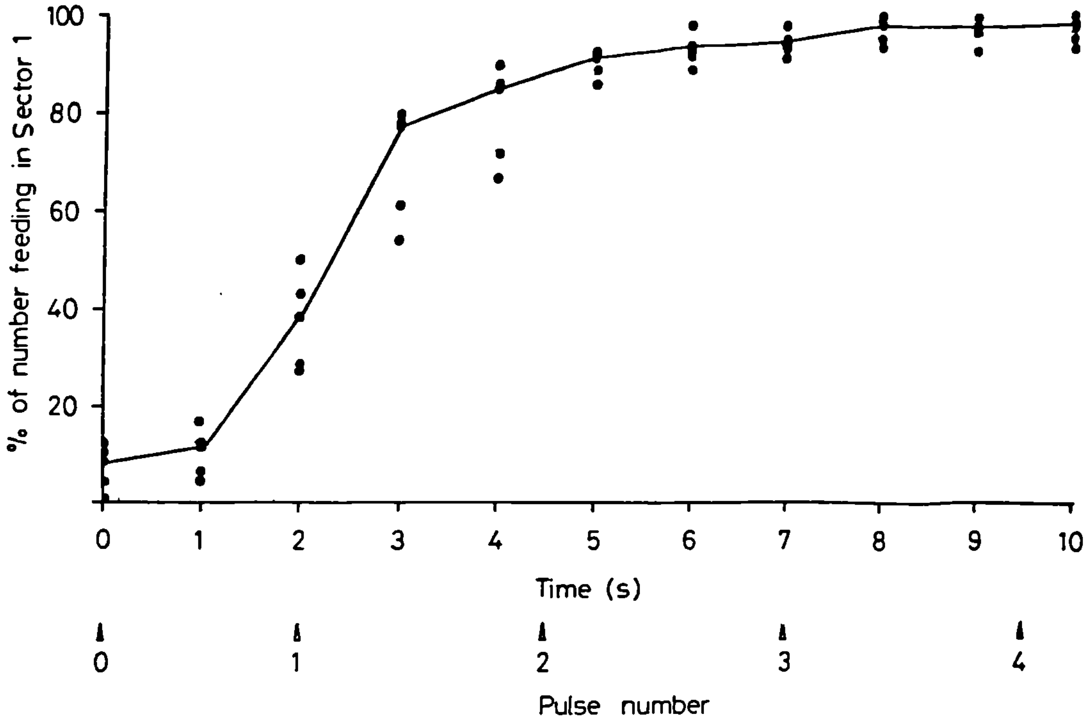


Figure 2.4. Well conditioned responses. The figure shows the change in the number of fish in Sector 1 at 1-s intervals throughout the conditioned stimulus (expressed as a percentage of the number feeding) during five separate trials in Conditioning Experiment 2. The line joins the medians and the arrows show the end of the pulse numbers.

NOTE: This percent response is a pooled measure which assumes that there are no variations in the strategies of the conditioned response.

number counted feeding. This procedure is considered valid because all fish had potential access to the food and so this percentage represents the proportion of individuals motivated to feed.

Figure 2.4 illustrates the time course of the conditioned response in five well conditioned responses. On the basis of these results, and to facilitate counting, the number in Sector 1 was counted only at the end of the 4th pulse of the conditioned stimulus and expressed as a percentage of the number of fish feeding in the net after the food delivery. This number was used as a measure of the degree of conditioning and is subsequently referred to as the percent response(see note on opposite page).

2.3.1.2.2. Results : the conditioned response

The results of the first four experiments are shown in Figure 2.5. Kendall's rank correlation coefficient, tau (Siegel, 1956), was used to investigate whether there was any significant correlation between trial number and the percent response during each experiment. The results of this analysis (Table 2.2) show that in all four experiments there was significant long term learning.

There was a considerable variation between experiments, probably because they were carried out in series and not in parallel. This variability made it difficult to carry out any valid statistical comparison between experiments. However, comparison of Experiments 2 (6 trials/day) and 3 (3 trials/day), which were carried out consecutively, showed least variation with both conditioning curves reaching a plateau of a greater than 85% response after 34 and 33 trials respectively. Thus, on the basis of these experiments, the rate of learning depends on the number of trials and not the time over which they are spread.

In three out of four experiments there was an erratic rise to a variable plateau of a greater than 75% response after 34 to 40 trials. Experiment 1 had

Table 2.2. Long-term learning during the conditioning experiments. The table shows the correlation between the percent response on each trial and trial number using Kendall's tau.

Conditioning Experiment	n	tau	significance level
1	27	0.328	$p < 0.05$
2	40	0.546	$p < 0.001$
3	41	0.627	$p < 0.001$
4	43	0.421	$p < 0.001$

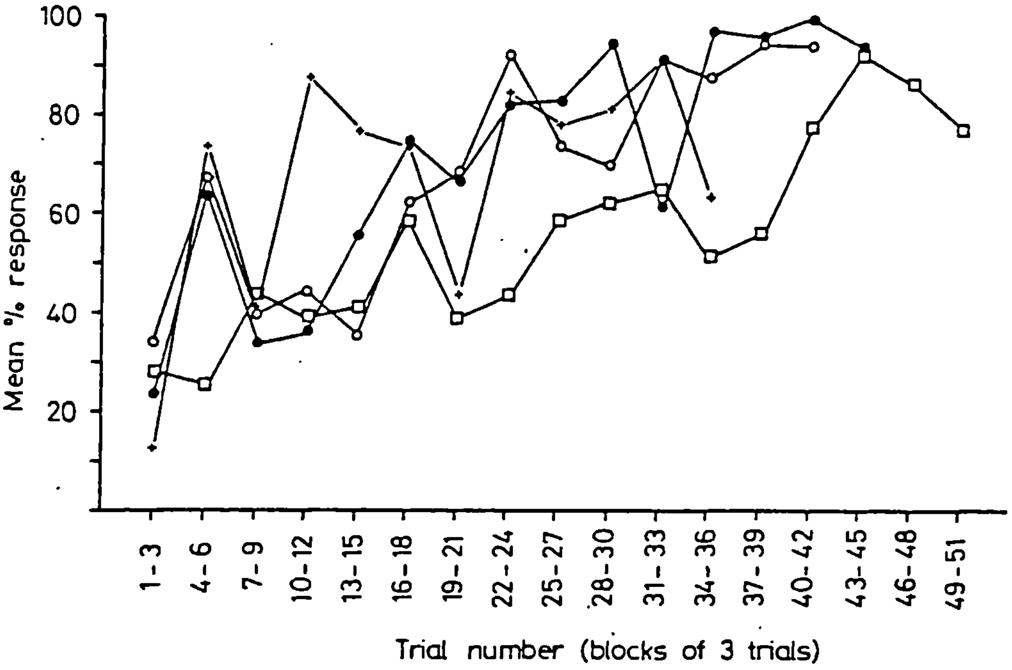


Figure 2.5. Conditioning curves for the 4 conditioning experiments.

+ shows Experiment 1, 6 trials per day.

o shows Experiment 2, 6 trials per day.

● shows Experiment 3, 3 trials per day.

□ shows Experiment 4, 6 trials per day.

to be discontinued before this plateau was reached although 100% responses were observed before trial 34. There was an increase in the activity of the group throughout conditioning (Section 2.3.1.3) and this behaviour introduced a considerable variation in the response as a result of fish being attracted to the activity of others in other sectors of the cage. This type of behaviour, which was stimulated during the conditioned stimulus, was the result of one or more individuals striking flotsam in mistake for food or splashing on the surface. These actions appeared particularly attractive to other fish, who were also excited by the sound and subsequently distracted from the feeding area. Fish eventually passed through this disruptive phase, however, and learnt to localize their activity closer to the feeding station.

The conditioning time was greater in Experiment 4. Fish appeared to be less motivated to feed during this experiment, taking longer to settle down in the experimental net and not rising as vigorously as they had done in the earlier experiments, which would have resulted in an increase in the conditioning time. This increase was probably due to the lower temperatures encountered during this experiment (9°C as opposed to 12-13°C in the earlier experiments). In addition, this experiment used the largest fish of this series of experiments (mean fork length = 263 mm) and thus they were physically unable to aggregate in as small an area as in the previous experiments and consequently the percent response in a well conditioned response was less. This result may have been due to size but may also have been aggravated by the larger fish spreading pellets outside the feeding area. In consequence their behaviour may have been reinforced over a wider area resulting in less of a tendency to aggregate than there had been in previous experiments.

The above experiment was therefore repeated in February/March (mean temperature = 6°C; range 5-6°C) with larger fish (mean fork length = 310 mm; s.d. = 13; n = 50) but with the feeding square built up to 15 cm above the water surface to minimize pellet loss. Fish in this experiment only consumed their allotted ration in one feed after 2 weeks in the experimental cage and never rose to food as well as the same stock of fish had done during the summer months. After 80 trials there was still no consistent aggregation around the feeding station although good aggregation (> 75% response) was occasionally observed. The results therefore suggest that long conditioning times were probably related to low feeding motivation at reduced winter temperatures.

2.3.1.2.3. Results : pre-trial behaviour

To determine whether the fish showed any tendency to aggregate in Sector 1 throughout the course of an experiment, the mean of the 6 pre-trial counts in Sector 1 was calculated for each trial in Experiments 1 to 4. Kendall's coefficient of rank correlation, tau, was then used to test the null hypothesis that there was no significant change in this mean with trial number in individual experiments. In Experiment 2 there was a significant negative correlation (tau = -0.223; $n = 41$; $p < 0.01$) and in Experiment 3 a significant positive correlation (tau = 0.285; $n = 41$; $p < 0.01$) between trial number and the pre-trial mean. There was no significant trend during Experiment 1 (tau = 0.071; $n = 27$; $p > 0.05$) and 4 (tau = 0.092; $n = 43$; $p > 0.05$). If the pre-trial mean was subtracted from the number in Sector 1 at the end of Pulse 4, however, there was still significant ($p < 0.05$) long term learning in all the experiments. Experiment 3, at 3 trials per day, was the longest in terms of time which may have encouraged fish to accumulate around the feeder although the results of the previous section (2.3.1.2.2.) suggested that it is the number of trials (food deliveries) and not the time over which they are spread which is important in the development of a conditioned response. In all experiments, however, fish were within visual range of the feeding station and therefore because they had easy access to food there was perhaps no necessity to remain very close.

The totals of the mean pre-trial numbers for each experiment are shown in Table 2.3. In all experiments groups of fish were significantly aggregated within the cage, although there was some tidal variation in the degree of aggregation (Appendix A). In individual experiments each group of fish returned to its preferred area after each trial as it was usually found there before the following trial. As a result of this behaviour there was no significant difference during any of the experiments between the numbers aggregating in Sector 1 on the different trials of each day (Wilcoxon test: 0930 versus 1054 pre-trial mean; $p > 0.05$; Friedman's two-way analysis of variance: 0930-1630 pre-trial means; $p > 0.05$; both tests from Siegel, 1956).

The preferred sectors were strikingly similar between all the experiments (Table 2.3). There was a significant similarity in the rankings between Experiments 1,2 and 4 (6 trials per day) (Kendall's coefficient of concordance; $W = 1.0$; $p < 0.001$). If Experiment 3 (3 trials per day) was included, however, the ranking was not significant ($W = 0.55$; $p > 0.05$) which was probably due to the tendency to aggregate near the feeder during this experiment. The reasons for the relatively consistent preference, in at least Experiments 1,2 and 4, are uncertain although Sectors 2 and 3 were probably more shaded than the others.

2.3.1.3. Development of the conditioned response : activity

2.3.1.3.1. Introduction and methods

Preliminary inspection of the data showed that there was also an increase in activity during the development of the conditioned response. Because the exact three dimensional position of a fish could not be recorded activity was measured indirectly by counting the total number of fish crossing the four sector boundaries (Figure 2.1) for 5 s after the onset of the conditioned stimulus. This time interval was chosen because preliminary analysis showed that in a well conditioned group of fish the activity, measured using this

Table 2.3. The sum of the pre-trial means in each sector during each of the conditioning experiments. Figures in parentheses show rankings. χ^2 is for a null hypothesis that fish were uniformly distributed throughout the four sectors. All χ^2, $p < 0.001$ (d.f. = 3).

Conditioning Experiment	Sector				
	1	2	3	4	χ^2
1	135 (4)	250 (1)	177 (2)	164 (3)	39.5
2	161 (4)	669 (1)	444 (2)	192 (3)	463.5
3	464 (1)	424 (2)	358 (3)	291 (4)	44.7
4	321 (4)	644 (1)	459 (2)	327 (3)	158.0

technique, declined after 5 s as fish aggregated close to the feeding station away from the sector boundaries. Control measurements were taken at 1- min intervals for 5 min prior to each trial by counting the number crossing the boundaries per 10 s and calculating the mean of these measurements.

There were some inherent errors in using the above method; measured activity would increase with depth, fish closer to the camera appearing, but not actually, being more active. This was probably not a serious source of error because most fish were aggregated within the top 50 cm of the water column (Appendix A). There would also be some error resulting from cage movement and differences in distance from the loudspeaker; fish closer having to cross fewer sector boundaries to move to the loudspeaker than those further away. Despite such limitations this technique did illustrate some aspects of the development of the conditioned response in terms of activity.

2.3.1.3.2. Results : the conditioned response

Consecutive Experiments 2 and 3 were analysed in this way because, apart from the difference in trial numbers per day, there was less disparity between the size of the fish and environmental conditions during these experiments. The results (Figure 2.6 a,b) show that a variable plateau of activity was reached in both experiments, before fish learnt to aggregate in Sector 1 (Figure 2.5), after approximately 10 to 12 trials. At this stage the fish were very active throughout the cage in response to the sound signal. There was a significant increase in activity during both Experiment 2 (tau = 0.241; $n = 40$; $p < 0.05$) and 3 (tau = 0.249; $n = 41$; $p < 0.05$).

The variation in trials per day had no obvious effect on the development of the response in terms of activity. Higher activity indices were recorded during Experiment 3 (3 trials/day), but this is probably because larger fish were used in this experiment (Table 2.1) and these larger fish were able to cover the cage quicker and thus appeared to be more active.

Figure 2.6. The development of the conditioned response in terms of activity.

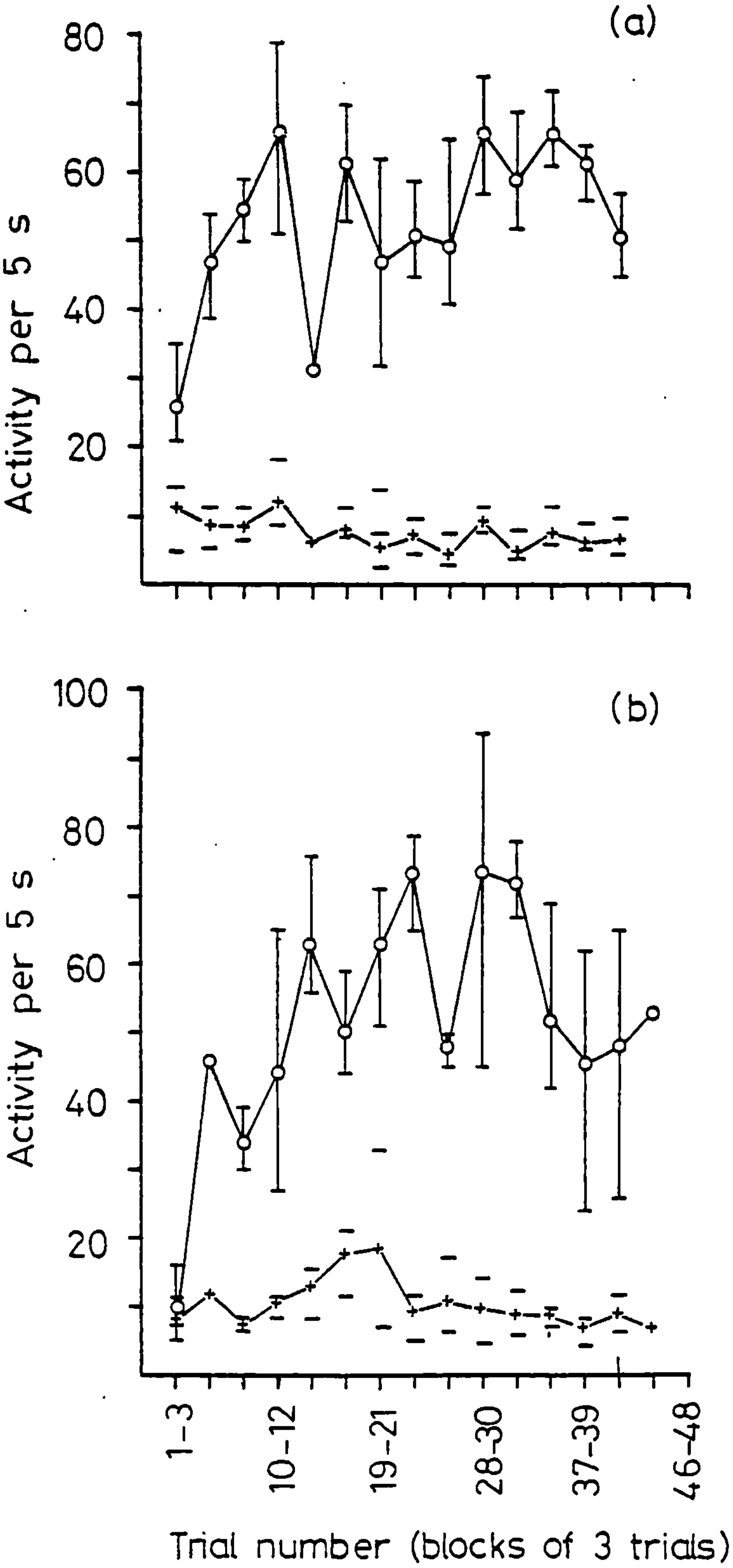
(a) shows Experiment 2, 6 trials per day.

(b) shows Experiment 3, 3 trials per day.

o represents the mean activity for the first 5 s of conditioned stimulus (± range).*

\+ represents the mean pre-trial activity per 5 s over the 5-min pre-trial period (± range).*

* The points without range bars represent single observations


(a)
80
60
40
20
Activity per 5 s
(b)
100
80
60
40
20
Activity per 5 s
1–3
10–12
19–21
28–30
37–39
46–48
Trial number (blocks of 3 trials)

Social facilitation was responsible for a large part of the activity because, as mentioned previously, fish were attracted to any individuals breaking the surface of the water or accelerating rapidly towards the surface. Any behaviour that resembled feeding would be attractive and because the sound signal conditioned such behaviour, socially mediated activity would be expected to increase during conditioning

2.3.1.3.3. Results : pre-trial behaviour

Kendall's tau was used to determine whether there was any significant change in pre-trial activity (mean of six 10- s intervals) during the course of each experiment. There was no significant change ($p > 0.05$) during any of the experiments and there was also no evidence of any significant difference in the activity on the different trials of each day (Wilcoxon test: 0930 trial versus 1054 trial; $p > 0.05$; Friedman's two-way analysis of variance: 0930-1630 trials; $p > 0.05$).

2.3.1.4. Development of the conditioned response : individual behaviour

2.3.1.4.1. Introduction and methods

To examine the development of the conditioned response in more detail the response of usually at least 20 individuals was observed in each clear trial during Experiment 2 (mean of 24.1 observations per trial; mode 20; range 16-34; 37 trials examined). Using the pause and slow playback facilities on the video tape recorders individual frames were stopped or played back slowly to follow the behaviour of individual fish. The behaviour of each was then categorized according to a scheme based on the behaviour observed in well conditioned responses. Details of these behavioural categories are illustrated in Figure 2.7 and outlined below:

A Pre-trial behaviour

1. Position : The cage was divided into a 16 cm x 16 cm grid on the video monitor screen. The position of the head of each fish within this grid was recorded immediately pre-stimulus.

Figure 2.7. The reactions and main subsequent behaviour types observed during Conditioning Experiment 2. Figures show tracings of the behaviour of fish at 500 ms intervals. Shaded fish indicate frames used to measure indicated timing criteria.* The polar angle (shown as dashed lines) is the angle subtended with respect to the loudspeaker in (a) and (b). Figures also show loudspeaker (l), feeding square (fs) and feeding area (fr). The latter encloses both the loudspeaker and the feeding ring.

(a) illustrates a positive reaction followed by direct movement to the loudspeaker.

(b) illustrates a neutral reaction followed by an indirect movement to the loudspeaker.

(c) illustrates a negative reaction followed by ex-area movement.

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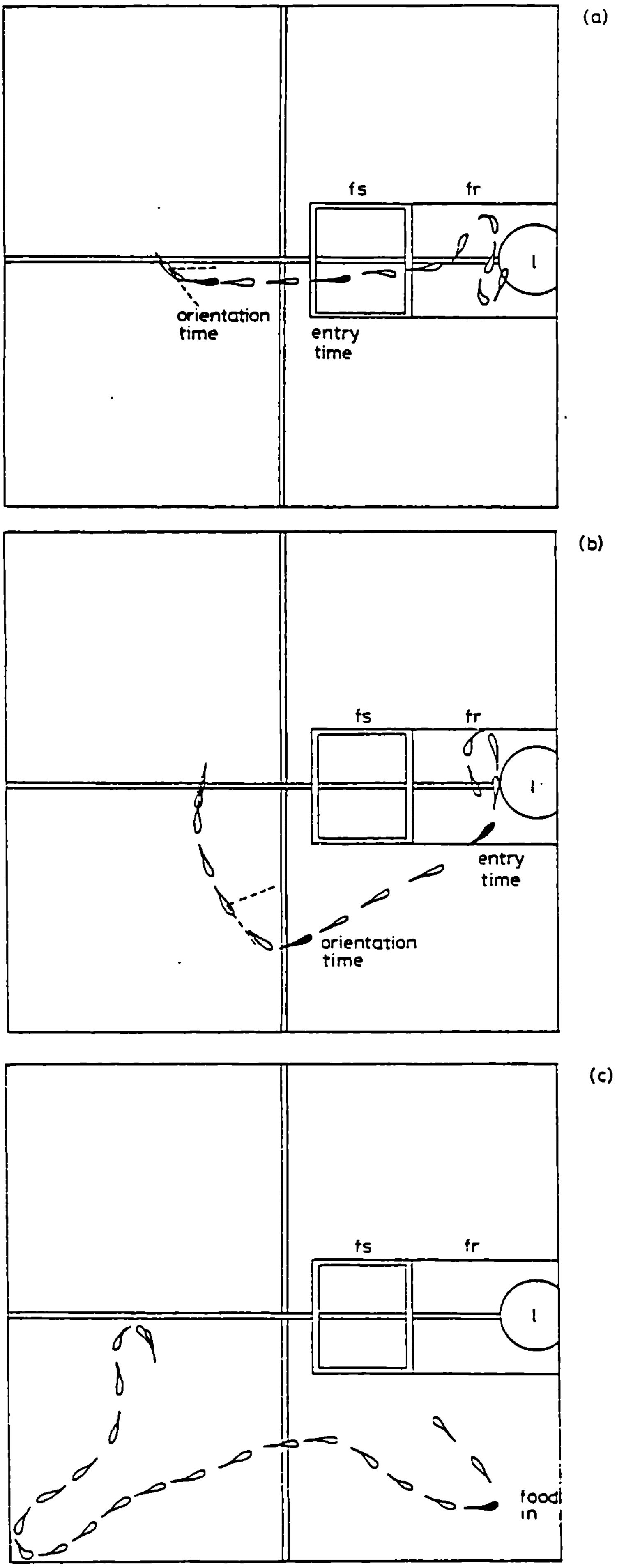
* The first trace in each diagram refers to the position of the fish at the start of the conditioned stimulus


(a)
fs
fr
l
orientation time
entry time
(b)
fs
fr
l
entry time
orientation time
(c)
fs
fr
l
food in

2. Angle : The angle of the fish, both with respect to the cage axis and the position of the loudspeaker (polar angle, Figure 2.7), was recorded immediately pre-stimulus.

B Initial reaction

1. Reaction time : Time taken to observe any perceptible response to the conditioned stimulus.

2. Reaction type : Categorized as follows:-

i negative - a turn away from the loudspeaker

ii neutral - no net movement with respect to the loudspeaker

iii positive - a turn towards the loudspeaker

iv no reaction - no perceptible change in behaviour

C Subsequent behaviour

1. Direct movement to the loudspeaker : Immediate movement, following a positive reaction, towards the area directly in front of the loudspeaker where it then showed a tendency to remain for a variable period of time (Fish facing the loudspeaker before the trial and moving directly to it were taken as reacting positively).

2. Direct movement to the feeding square : As above but towards the area beneath the feeding square.

3. Indirect movement to the loudspeaker : Neutral reaction or exploratory type behaviour prior to moving to the loudspeaker as defined in 1.

4. Indirect movement to the feeding square : As 3 but towards feeding square as in 2.

5. Ex - area movement : No movement into the areas designated by 1-4.

The timing of the subsequent behaviour was investigated by measuring:-

1. Orientation time : Time from the start of the conditioned stimulus until the fish was pointing towards its destination as designated in C, 1-4.
2. Time taken to enter feeding area : Time taken for tail to cross the boundary of the feeding area.

Where possible it was also recorded whether the fish fed or not.

2.3.1.4.2. Results : pre-trial position and behaviour

To analyse the effect of position on the reaction type the video monitor was divided into two halves, one near (H_1) and one on the opposite side from the loudspeaker (H_2). The number of different reaction types observed within each half of the screen, during the whole of Experiment 2, are shown in Table 2.4. The data from Table 2.4 were then used to compare the distribution of different reaction types with one another. Contingency tables were constructed and χ^2 calculated for each pair of reaction types. Fisher's exact probability test for 2 x 2 contingency tables (Siegel, 1956) was used where the expected values for χ^2 were less than five.

The results show that there were a significantly greater proportion of negative reactions closer to the loudspeaker than any other reaction type ($p < 0.001$). This is probably because fish were more likely to show a startle (negative) reaction to the higher amplitude stimulus within H_1. There were no significant differences between the distribution of other reaction types although video tape observations showed that non-reactors were often found away from the main group of fish where they were probably less prone to excitation through social facilitation.

Table 2.4. The frequency of occurrence of the different reaction types in the two halves of the experimental cage. H_1 = half of cage with feeding station ; H_2 = other half. The data derive from Conditioning Experiment 2.

Reaction type	Number of fish H_1	 H_2
Positive	115	342
Neutral	96	227
Negative	52	38
No reaction	1	14
Total	264	621

The direction in which the fish was pointing with respect to the loudspeaker affected the time taken to orientate to the loudspeaker during direct responses. The relationship between orientation time (minus reaction time) (R, s) and polar angle (P, deg) could be expressed by the significant linear regression:

$$R = 0.0054\,P + 0.083$$

$$t = 5.668;\ d.f. = 69;\ p < 0.001.$$

(The data derive from trials 32 to 42 inclusive and only consider fish within the undistorted areas of the video picture (Section 2.2.2.)). This result is to be expected because fish facing away from the loudspeaker must have taken longer to turn to face it.

The polar angle could also have influenced the reaction and subsequent behaviour type. This aspect was investigated by counting the number of direct and all indirect types of behaviour in 30° class intervals from polar angles 0° to 180° using data from trials 32 to 42 inclusive. A contingency table was constructed with this data, but there was no significant difference ($\chi^2 = 10.119$; d.f. = 5; $p > 0.05$) between the proportion of behaviour types in different polar angle classes. Thus, the variation in behaviour types (which are to be discussed) were not due to differences in polar angle.

2.3.1.4.3. Results : initial reaction type and reaction time

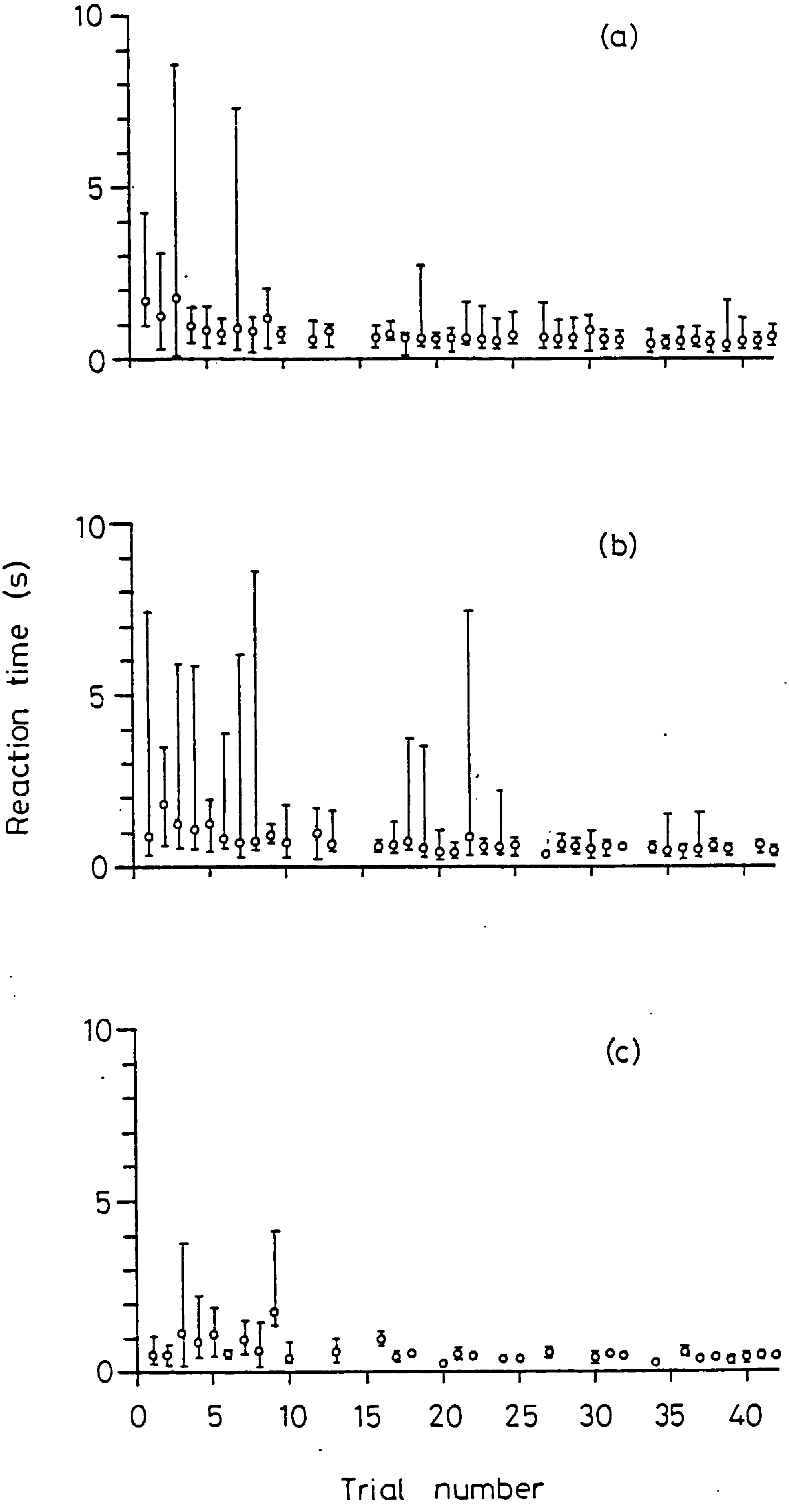
In trial 1 there was a significantly greater proportion of negative reactors in H_1 than all the other reaction types combined (Fisher's exact probability test for χ^2; $p = 0.008$). The Mann-Whitney U test (Siegel, 1956) also showed that in this trial there was a significant difference in the median reaction time of negative (median = 0.47 s; n = 7) and positive and neutral reactors combined (median = 0.90 s; n = 23) ($T = 50.5$; $n_1 = 7$; $n_2 = 23$, $p < 0.01$) (Figure 2.8). This result suggests that the sound stimulus provoked an unconditioned startle response in fish close to the loudspeaker and that fish further away reacted to the startled fish rather than the sound stimulus.

Figure 2.8. The change in median and range of reaction times of the three reaction types during Conditioning Experiment 2.

(a) positive reactions

(b) neutral reactions

(c) negative reactions


(a)
(b)
(c)
Reaction time (s)
0
5
10
Trial number
0
5
10
15
20
25
30
35
40

To examine whether there were any consistent differences between the reaction times of the three different reaction types the median reaction times of each type were calculated for each trial and compared over the whole experiment using Friedman's two-way analysis of variance (Siegel, 1956). There was a significant difference between the median reaction times throughout the experiment ($\chi^2_T = 17.53$; d.f. = 2; $p < 0.01$) as a result of the consistently lower median negative reaction times (Figure 2.8).

2.3.1.4.4. Results : changes in reaction time and type during conditioning

To quantify the change in the reaction time of each reaction type during conditioning, the median reaction time of each reaction type was computed on each trial (Figure 2.8). Kendall's tau was then used to test the observed distribution against the null hypothesis that there was no significant change in the median reaction time, of individual reaction types, with trial number. The results (Table 2.5) show that there was a significant decrease in the median reaction time, of all the different reaction types, during the experiment.

There was also a significant increase in the proportion of positive reactions and decrease in the proportion of negative and non-reactors during conditioning (Table 2.6). These results suggest that fish are learning to react positively, rather than negatively or not at all, during conditioning although the decrease in the proportion of non-reactors may also have been due to the increased activity of a conditioned group. Not all reactions were subject to change as a result of learning because some fish close to the loudspeaker consistently performed negative startle reactions throughout the course of the experiment. There was also no significant change in the proportion of neutral reactors. This latter feature will be discussed in further detail in relation to the subsequent behaviour that is described in the following section.

Table 2.5. The change in the median reaction time during conditioning. The table shows the correlation between the median time on each trial and trial number using Kendall's tau.

Reaction type	tau	n	p
Positive	- 0.62	37	< 0.001
Neutral	- 0.58	36	< 0.001
Negative	- 0.40	31	< 0.01

Table 2.6. The change in the proportion of different reaction types during conditioning. The table shows the correlation between the proportion of each reaction type on each trial and trial number using Kendall's tau.

Reaction type	tau	n	p
Positive	0.246	37	< 0.05
Neutral	-0.108	37	> 0.05
Negative	-0.387	37	< 0.01
Non-reactors	-0.817	37	< 0.001

2.3.1.4.5. Results : changes in subsequent behaviour during conditioning

Figure 2.9 shows the changes in the behaviour that followed the initial reaction during conditioning. There was an initial peak in the proportion moving both directly and indirectly towards the feeding square, but significant decline throughout the whole experiment (Table 2.7). The significant increase (Table 2.7) in the proportion moving both directly and indirectly towards the area of the loudspeaker suggests a shift in the attention of the fish from the feeding point towards the source of the conditioned reinforcer (sound source). There was also a significant decrease in the median orientation time of fish moving directly (tau =-0.337; n = 33; $p < 0.01$) and indirectly (tau = -0.235; n = 36; $p < 0.05$) towards the loudspeaker during the experiment. There was a similar significant decrease in the median entry time of fish moving directly (tau = -0.473; n = 33; $p < 0.001$) and indirectly (tau = -0.235; n = 36; $p < 0.05$) towards the loudspeaker during the experiment. These results show how the timing of the conditioned response improves through learning and this was particularly obvious for indirect fish who took much more tortuous indirect routes during the early stages of conditioning.

The median orientation time (to the loudspeaker) of direct fish was significantly less than that of indirect fish throughout the whole experiment (Wilcoxon test: T = 0; N = 33; $p < 0.01$) suggesting that the subdivision into these two main subsequent behaviour types was justified. Furthermore, the median entry times of positive/direct reactors were significantly less throughout the course of the experiment (T = 0; N = 33; $p < 0.01$) suggesting that the direct fish may be able to mediate the responses of some indirect fish by attracting them towards the feeding area.

Figure 2.9 shows that, although there was a significant increase in the proportion of fish moving directly to the loudspeaker throughout the experiment, there was no further increase after trial 32. This 'plateau',

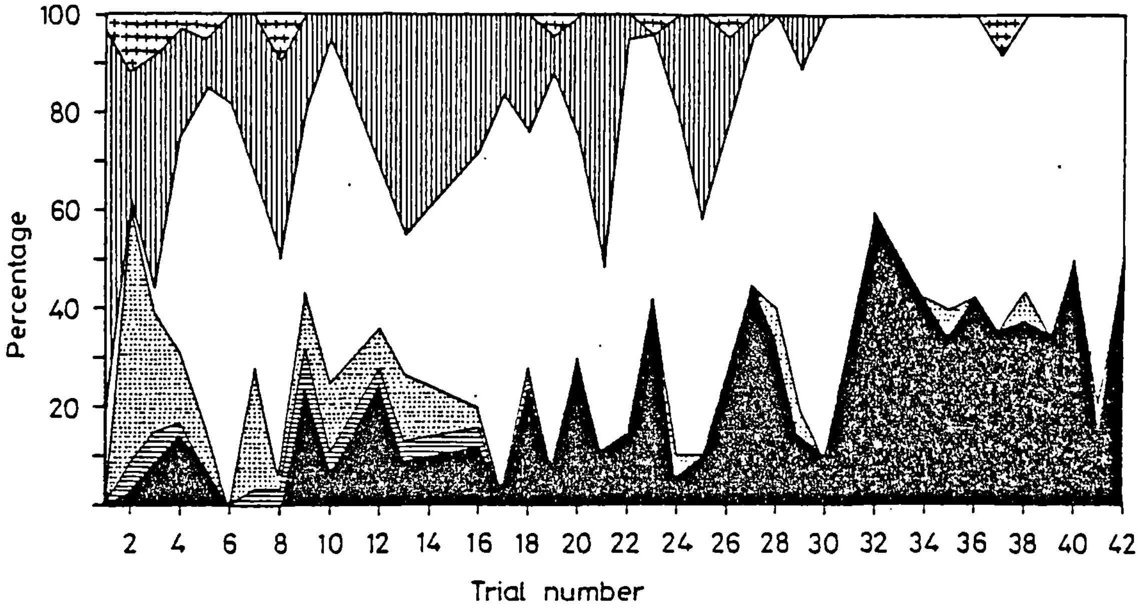


Figure 2.9. The change in the proportion of different subsequent behaviour types during Conditioning Experiment 2.

⊞ no reaction

▥ ex-area movement

□ indirect to loudspeaker.

⊡ indirect to feeding square.

⊟ direct to feeding square.

■ direct to loudspeaker.

Table 2.7. The change in the proportion of different subsequent behaviour types during conditioning. The table shows the correlation between the proportion of each subsequent behaviour type on each trial and trial number using Kendall's tau.

Subsequent behaviour type	tau	n	p
Direct to loudspeaker	0.546	37	< 0.001
Direct to feeding square	-0.871	37	< 0.001
Indirect to loudspeaker	0.240	37	< 0.05
Indirect to feeding square	-0.625	37	< 0.001
Ex-area movement	-0.721	37	< 0.001
No reaction	-0.817	37	< 0.001

between trials 32 and 42, may represent a transitional phase prior to all fish learning to move directly to the loudspeaker, or it may represent a consistent subdivision into direct and indirect responses within the conditioned group. In the previous section there was no change in the proportion of neutral reactors suggesting that such behaviour may be a relatively constant feature of the group. In the experiments of Section 2.3.1, which were continued to over 100 trials, indirect behaviour was also observed. Thus, there was some evidence to suggest that there will always be a variation in the behavioural types within a conditioned group of fish.

2.3.1.5. The cues involved in mediating the conditioned response

2.3.1.5.1. Introduction and methods

To investigate the relative importance of acoustic and visual cues in mediating the conditioned response, the spatial arrangement of the loudspeaker, the feeder and feeding square and a dummy loudspeaker was randomly changed in several trials at the end of Experiments 1, 2 and 3. A 10-s conditioned stimulus was given as usual, but fish were reinforced 5 min later so as not to reinforce a particular configuration, but to provide constant motivation and allow the results to be expressed, as usual, as a percentage of the total number feeding. Trials with different configurations were carried out in a random order with each change in configuration being preceeded by a trial in the normal (conditioning) configuration, but including a dummy loudspeaker on the opposite side of the cage. No dummy was included during conditioning or the experiments at the end of Conditioning Experiment 1. To preclude any orientation to subtle differences between the covering of the dummy and live loudspeakers, fresh polythene covers were added to both before these experiments.

2.3.1.5.2. Results : responses to the novel positions

Figure 2.10 shows the gross features of the responses to the three different novel configurations of the experimental apparatus. To quantify the differences between each novel configuration and the preceeding normal trial, the number of fish in Sectors 1 and 3 was counted at the end of each pulse of the conditioned stimulus in each trial. The number of fish within each sector at the end of each pulse was then summed for the whole trial (four pulses) and the observed proportion within these sectors on each novel trial tested against the two following null hypotheses using χ^2:

1. That there was no significant difference between the proportion of fish in Sectors 1 and 3 during the conditioned stimulus in the novel and immediately preceeding normal trial.
2. That there was no significant difference between the proportion of fish within Sectors 1 and 3 during the conditioned stimulus in the novel trial, and the numbers in Sectors 3 and 1 respectively during the preceeding normal trial. This hypothesis compares the observed reaction to the novel position with that expected if the fish were conditioned to aggregate in Sector 3 and not, as during these experiments, in Sector 1, i.e., it assumes that if fish were conditioned in Sector 3 the response would be a mirror image of that observed on the previous normal trial in Sector 1. If H_0 is not rejected then the fish showed no affinity to Sector 1 with the apparatus in a particular novel position.

The results of this analysis are shown in Table 2.8. Individual experiments have been treated separately and in addition all normal trials in each experiment were tested against each other using χ^2. There was no significant difference (p > 0.05) between any normal treatments during each conditioning experiment showing that the results presented in Table 2.8 were primarily due to the changes in the configuration of the experimental apparatus.

Figure 2.10. The reaction of conditioned rainbow trout to different configurations of the experimental apparatus. The training configuration is given in (a) and the subsequent configurations are described by the symbols :

● for "live" loudspeaker

○ for "dummy" loudspeaker

☐ for feeder and feeding square

Sector 1 on RHS and Sector 3 on LHS of cage as shown. Graphs show the number of fish in Sector 3 (+) and Sector 1 (o) at the end of each pulse expressed as a percentage of the number feeding at the end of each trial. Each point is the mean of 3 experiments (a, n = 9; b,c,d,n = 3). The point at Pulse 0 represents the 5-min pre-trial mean.

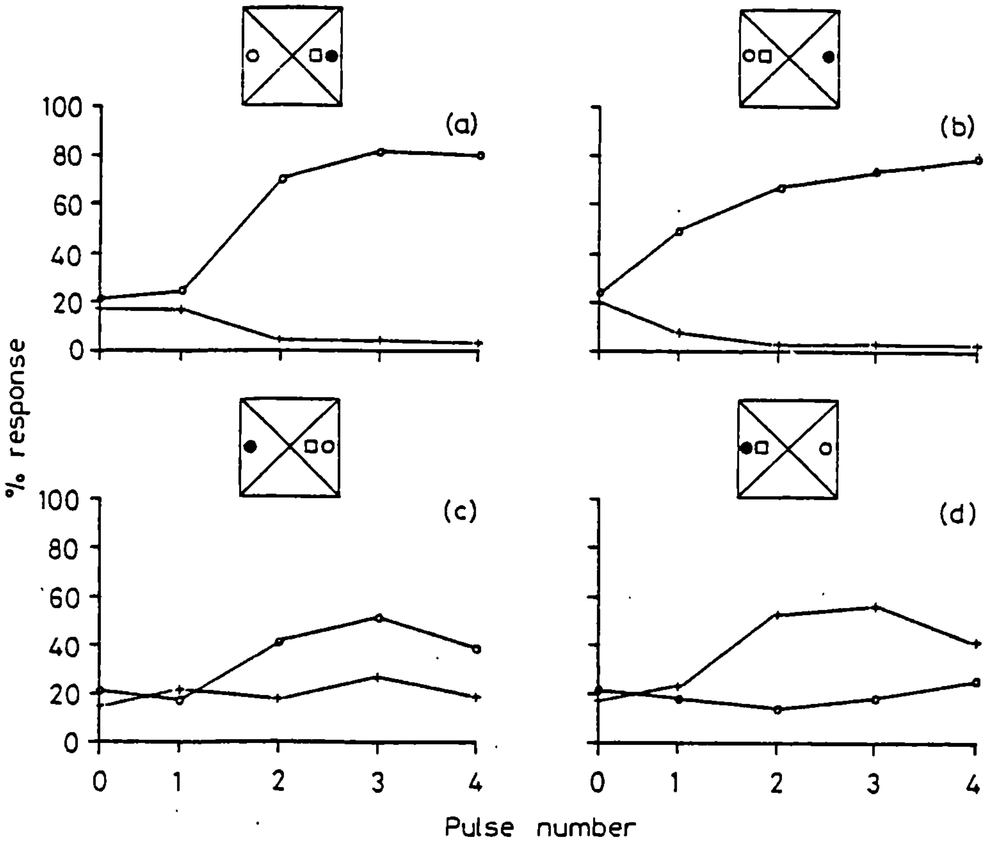

(a)
(b)
(c)
(d)
100
80
60
40
20
0
0
1
2
3
4
% response
Pulse number

Table 2.8. χ^2 values associated with the testing of the response to the novel configurations (b, c, d) against the two null hypotheses (1 and 2). See text and Figure 2.10 for further details. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; rest, $p > 0.05$.

	Configuration versus Null Hypothesis 1 or 2					
Conditioning Experiment	(b)v1	(b)v2	(c)v1	(c)v2	(d)v1	(d)v2
1	1.77	145.96***	29.50**	79.07***	76.89***	4.54*
2	4.00*	190.72***	35.74***	130.04***	112.66***	56.83***
3	2.13	106.97***	26.89***	64.36***	96.47***	2.24

The results show that whenever the "live" loudspeaker was placed on the opposite side of the cage, there was a significant movement out of Sector 1 into Sector 3 (Table 2.8; Column (c)vl, (d)vl). Figure 2.10b and Table 2.8 (Column (b)vl) show that the visual stimuli of the experimental apparatus alone accounts for only a small (but just significant on one occasion in Experiment 2) part of the attraction. Thus, the acoustic stimulus and the direction from which it originated was the most important cue used in mediating the conditioned response.

Moving the loudspeaker with the feeder and feeding square had a more significant affect on the numbers attracted to Sector 3 than moving the loudspeaker alone. This result suggests that the more visual stimuli, originally associated with Sector 1, that were transported to Sector 3, the more fish that were attracted to the novel position. On only one occasion, however, was the response as good as expected if the fish showed no affinity to Sector 1 (i.e., as expected with Null Hypothesis 2). Thus, the visual cues associated with the experimental apparatus and the cage environment were also important in mediating the response.

2.3.1.5.3. Results : initial reactions to the novel positions

The aim of this section was to show how the initial reaction (Section 2.3.1.4.) was modified by the different configurations of the experimental apparatus. The data derive from Conditioning Experiment 2. The initial reaction of fish to the sound stimuli was categorized, as in Section 2.3.4.1., as either positive, neutral or negative with respect to the "live" loudspeaker position (Table 2.9). χ^2 analysis was then used to compare the frequency of occurrence of the different reaction types to the various configurations.

There was no significant difference in the proportion of different reaction types in configuration (c) and (d) ($\chi^2 = 1.381$; d.f. = 2; $p > 0.1$) and therefore these two sets of data were combined to avoid violating the conditions of χ^2

Table 2.9. The frequencies of different reaction types in response to different configurations of the experimental apparatus. The reactions to each configuration are shown with the immediately preceeding normal (a) trial. Details of the experimental configurations are given in Figure 2.10.

	Reaction Type			
Configuration	Positive	Neutral	Negative	Total
(a)	15	7	2	24
(b)	15	10	2	27
(a)	18	8	2	28
(c)	11	9	11	31
(a)	21	9	0	30
(d)	13	8	7	28

(expected < 5) in the subsequent analysis. The data of the reactions to configuration (a) were similarly combined. There was a highly significant difference between these two data sets ($\chi^2 = 18.831$; d.f. = 2; $p < 0.001$) which arose from an increase in the proportion of negative reactions as well as a decrease in the proportion of positive reactions to the novel loudspeaker position. These results suggest that, although some individuals turned towards the "live" loudspeaker in the novel position, some also turned towards the previously conditioned loudspeaker position. Thus, previously learned visual cues, as well as directional cues associated with the acoustic stimulus, were used to mediate the initial reaction to the conditioned stimulus.

There was no significant differences between the frequency of occurrence of the reaction types to configuration (b) and (a) (combined) ($\chi^2 = 0.975$; d.f. = 2; $p > 0.1$) showing that the site of the feeding station alone, in the novel position, did not influence the initial reaction to the acoustic stimulus.

2.3.1.5.4. Results : changes in subsequent behaviour

The aim of this section was to examine how the fish behaved after their initial reaction. The data derive from Conditioning Experiment 2. The number of fish moving across the four sector boundaries towards and away from the "live" loudspeaker were counted on each trial, both for 5 min prior to the conditioned stimulus (for 10 s periods at 1 min intervals) and between 0 and 5 s and 5 and 10 s after the onset of the conditioned stimulus. The observed distributions were then tested (using χ^2) against the null hypothesis that there was no preferred direction of travel.

The results are shown in Table 2.10. There was a significant movement towards the "live" loudspeaker during the first 5 s of the conditioned stimulus in all cases. Greater χ^2 values were observed with the normal configuration than any other suggesting a smaller net movement towards the "live" loudspeaker when the configuration of the apparatus was altered. In configuration (c) a net

Table 2.10. The response to different configurations of the experimental apparatus showing the χ^2 associated with the null hypothesis that there was no net movement across the sector lines in any one direction. The reaction to each configuration is shown with the immediately preceeding normal (a) trial. Details of the configurations are given in Figure 2.10.

(+) = net movement towards "live" loudspeaker

(-) = net movement away from "live" loudspeaker

***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; rest, $p > 0.05$

Configuration	Pre-trial behaviour	Behaviour during the conditioned stimulus 0 - 5 s	5 - 10 s
(a)	1.09 (-)	34.91 (+)***	0.55 (+)
(b)	0.66 (-)	20.93 (+)***	1.49 (+)
(a)	0.00	36.12 (+)***	0.00
(c)	1.35 (+)	4.33 (+)*	46.75 (-)***
(a)	0.73 (-)	36.97 (+)***	0.07 (+)
(d)	0.01 (-)	10.01 (+)**	0.61 (-)

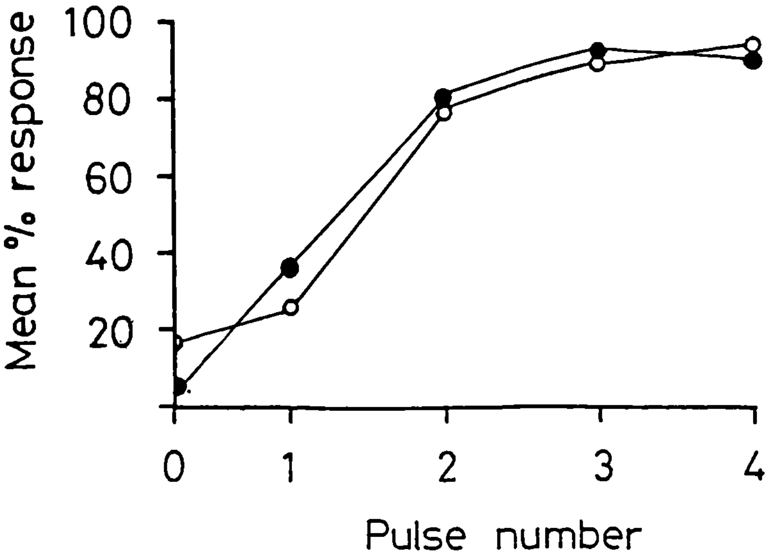


Figure 2.11. The conditioned response before (o) and after (●) 24 days without any conditioned stimulus. Response measured as the number moving into Sector 1 expressed as a percentage of the number feeding. The point for Pulse 0 represents the 5 min pre-trial mean. The data derive from the 6 trials before and the 3 trials after 24 days.

movement back towards the original training position was observed after 5 s again illustrating the importance of the visual cues associated with this original site.

2.3.1.6. Food only control experiments

To ensure that no extraneous cues were influencing the fish during the conditioning experiments a trial was carried out at the end of each experiment with the loudspeaker disconnected. No reaction was observed during the period when the conditioned stimulus would have been on, showing that no extraneous cues were involved.

2.3.1.7. Memory

At the end of Experiment 2 the use of the conditioned stimulus was discontinued and the fish were fed by hand once per day for 24 days. The fish remained in the experimental cage throughout this period. On the 25th day, three trials were carried out as normal to investigate the retention of the conditioned response.

Figure 2.11 depicts the conditioned response both prior to and after 24 days. This result suggests that there was no loss of memory over this period.

2.3.2. Conditioning experiments in the long net

2.3.2.1. The development of the conditioned response in the long net (Experiment 5)

2.3.2.1.1. Introduction and methods

The aim of this experiment was to compare the learning rate of fish within the larger enclosure with that of fish within the small net. A diagram of the experimental apparatus illustrating the relevant cage numbering is shown in Figure 2.12.

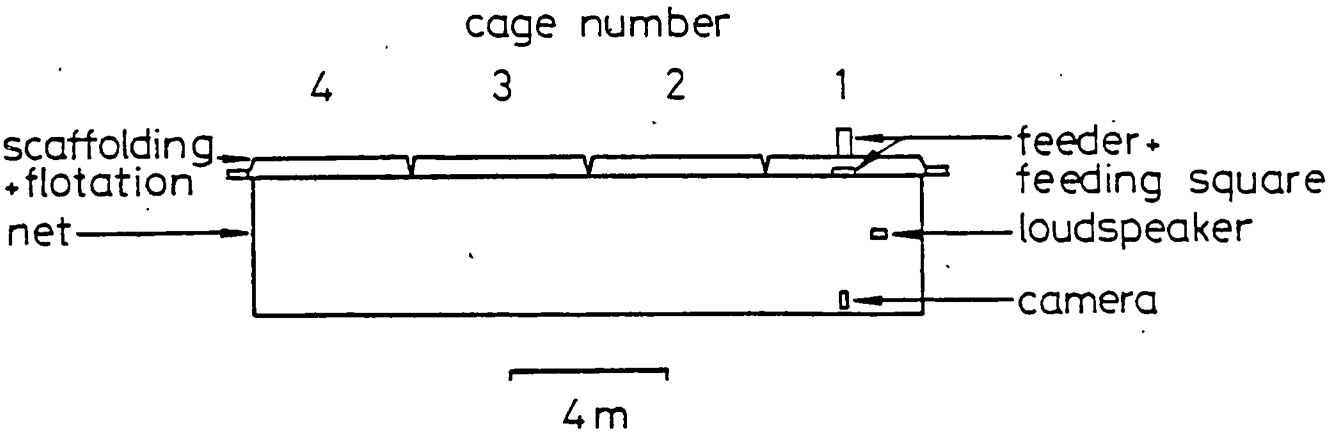


Figure 2.12. Lateral view of the experimental cages used during the long net experiments (Experiments 5,6) and the number of separate cages referred to in the text. Fish were free to swim between the four cages.

The duration of the conditioned stimulus was kept at 10 s to ensure the present experiments were comparable with Experiments 1 - 4. Theoretically, a fish at the far end of the cage would have to travel at a mean velocity of 1.37 $m.s^{-1}$ to be seen in Cage 1 at the end of Pulse 4 of the conditioned stimulus. This velocity is considerably below the maximum sustainable speed of a 21-cm rainbow trout (2.25 $m.s^{-1}$; Bainbridge, 1961) suggesting that,in theory at least, the experimental fish were capable of swimming this distance in the allotted time.

For analysis, the number of fish in Cage 1 was counted every minute for 5 min prior to the experiment and at the end of Pulse 4 of the sound stimulus. The maximum number seen in Cage 1 within 1 min of feeding was also recorded. To estimate the degree of aggregation around the feeding station a square was marked on the video monitor which corresponded to a 1.2m x 1.2m area at the water surface centred on the middle of the transducer, 0.75 m from the centre of Cage 1. The number of fish within this area was also counted at the above times.

2.3.2.1.2. Results: the conditioned response

The experiment was continued for 105 consecutive trials with the camera in Cage 1. There was a significant correlation between trial number and the number in Cage 1 at the end of Pulse 4 (tau = 0.377; n = 103; $p < 0.01$) over the first 105 trials showing that, like Experiments 1 - 4, there was a significant long term learning trend. However, a feature of the results which was obviously different (Figure 2.13) was the significantly lower number of fish responding on Pulse 4 on the first trial of the day (0930) when compared with the last trial of the previous day (Wilcoxon test : T = 6.5; N = 17; $p < 0.01$). The response to the 0930 trial was also the lowest response of each day (Friedman's two way analysis of variance; $\chi_r^2 = 36.267$; d.f. = 5; $p < 0.001$). There were also significantly less fish feeding on the 0930 trial when compared with the last

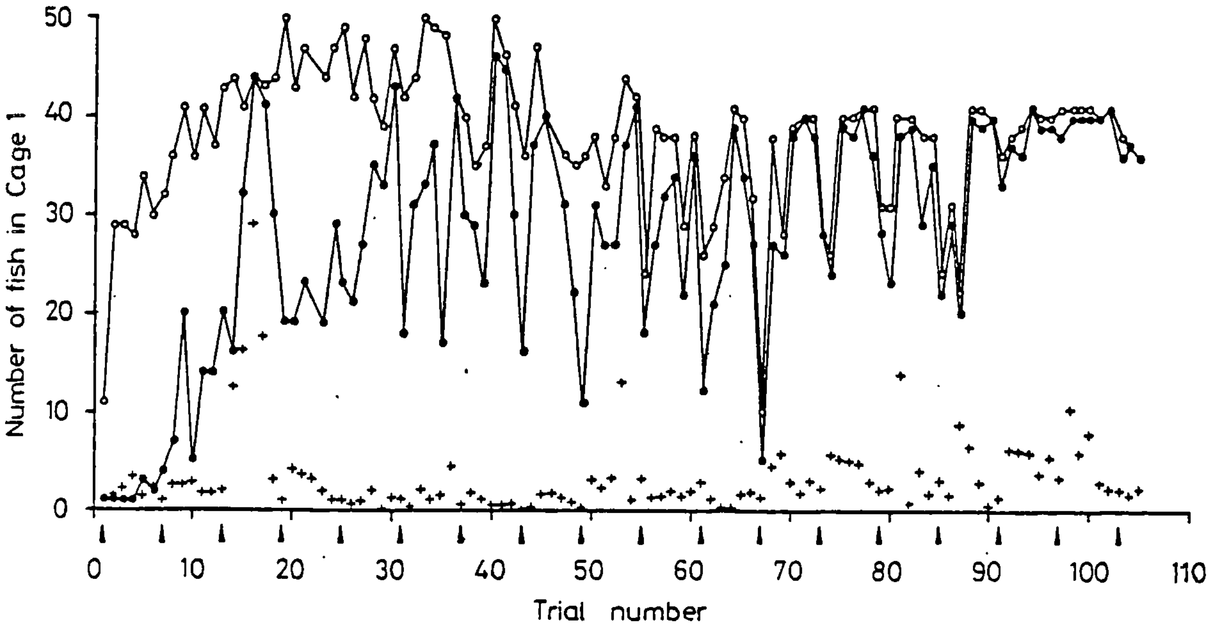


Figure 2.13. The development of the conditioned response during Experiment 5.

o shows the maximum number feeding in Cage 1 during 1 min post-feeding.

● shows the number at the end of Pulse 4 of the conditioned stimulus.

+ shows the 5-min pre-trial mean of the numbers in Cage 1.

Arrows indicate 0930 trials.

trial of the previous day ($T = 29.5$; $N = 17$; $p < 0.05$) and again, less fish fed at 0930 than on any other trial during the day ($\chi_r^2 = 14.552$; d.f. = 5; $p < 0.02$). This poor 0930 behaviour was probably due to fish moving away from the feeding area overnight and the subsequent improvement was due to the fish remaining close to the feeding station after this early feed. This interpretation is also borne out by the fact that the 0930 pre-trial mean was the lowest of the day ($\chi_r^2 = 12.185$; d.f. = 5; $p < 0.05$). As a consequence of this behaviour the 0930 trial was considered to be a good indicator of the state of conditioning during this experiment.

The 0930 response is shown separately in Figure 2.14 and suggests that conditioning was complete after 97 trials, but also shows that there was a variation in the numbers attracted to the feed on these 0930 trials during the course of the experiment. This number, after an initial maximum on trial 19, decreased until trial 67 and then subsequently improved until a plateau was reached after trial 97 when at least 36 fish (88% of the number removed from the net at the end of the experiment) were recorded on each 0930 trial (Figure 2.14). Unfortunately, nine fish were lost during the course of the experiment and so the final plateaux in Figures 2.13 and 2.14 do not reach 50.

The variation in the number of fish feeding on the 0930 trial can be explained in terms of a change in the distribution of fish in the net during the experiment. The initial high numbers attracted around trials 19 and 25 were obviously attracted relatively efficiently, either because they were aggregating close to the feeding station or, more likely, because fish did not enter Cage 1 en masse, because they were relatively evenly distributed throughout the net; in both situations fish would have been easily attracted to feed because most individuals were within visual contact with other fish. The net decline in the number attracted to feed between trials 19 and 67 was probably due to a visually isolated and distinct group of fish forming near the feeding station,

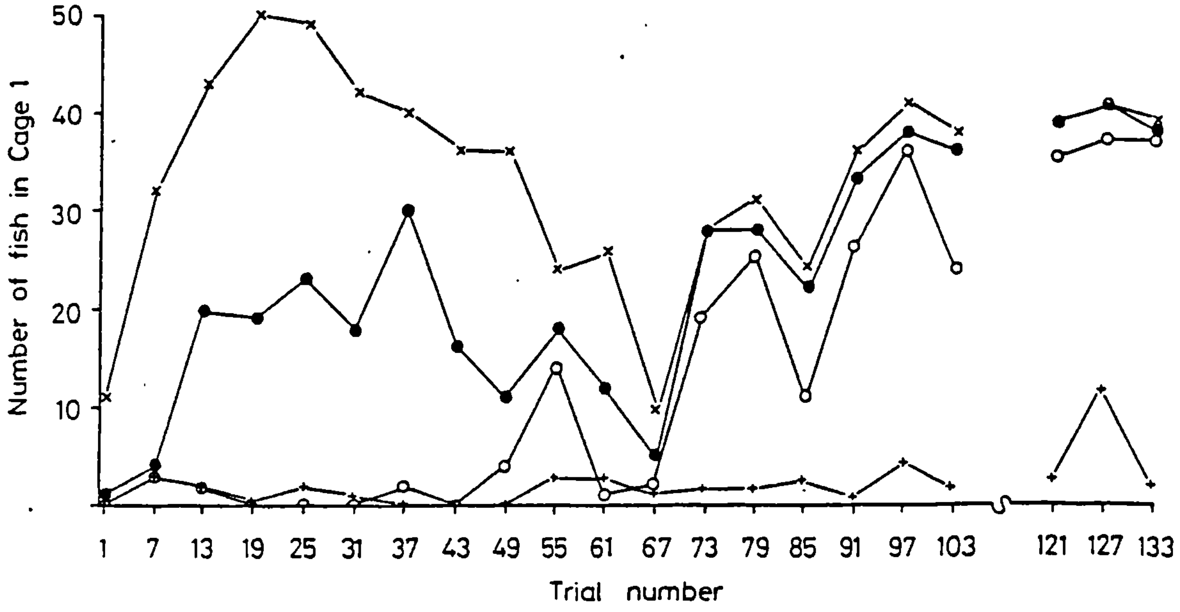


Figure 2.14. The development of the conditioned response during Experiment 5 as measured on the 0930 trial of each day.

X shows the maximum number feeding in Cage 1 up to 1 min post-feeding.

● shows the number in Cage 1 at the end of Pulse 4.

o shows the number aggregating around the feeding station at the end of Pulse 4.

+ shows the 5-min pre-trial mean.

which would have reduced the efficiency with which fish further away from the feeding station were attracted to feed. The increase in the number feeding after trial 67 would then have been due to both an improved ability to respond to low amplitude conditioned stimuli (further away from the loudspeaker) and to an increase in the number of fish remaining close to the feeding station. In fact, both probably occurred as there was a significant increase in the number remaining close to the feeding station throughout the experiment (Section 2.3.2.1.4).

2.3.2.1.3. Results: aggregation around the feeding station

There was a significant improvement in the degree of aggregation throughout the first 100 trials (tau = 0.500; n = 99; $p < 0.001$) (Figure 2.14). The response was, however, inconsistent because, within the first 100 trials, fish were often attracted to flotsam or other fish appearing to feed in Cage 1. Similar behaviour has also been described in Section 2.3.1., although unlike these small net experiments, fish did not pass this behavioural phase within 100 trials in the long net. The response was considerably improved, however, by extending the length of the sound signal from 10 to 30 s (Figure 2.15). This length of signal allowed fish to be active throughout the cage prior to aggregating around the feeding area and so, from trial 100 onwards, the signal remained at 30 s. This lengthening of the signal resulted in a more consistent aggregation throughout the conditioned stimulus, perhaps because fish were rewarded after settling down around the feeding point and not during a poorly localized feeding frenzy in another part of the cage.

The aggregative behaviour consisted of a tight circular (anticlockwise and clockwise was observed on different occasions) movement around the ropes suspending the loudspeaker. To investigate the depth of this reaction the camera was placed horizontally at a depth of 1 m, 1.5 m away from the loudspeaker so that both the loudspeaker and feeding ring were within the field

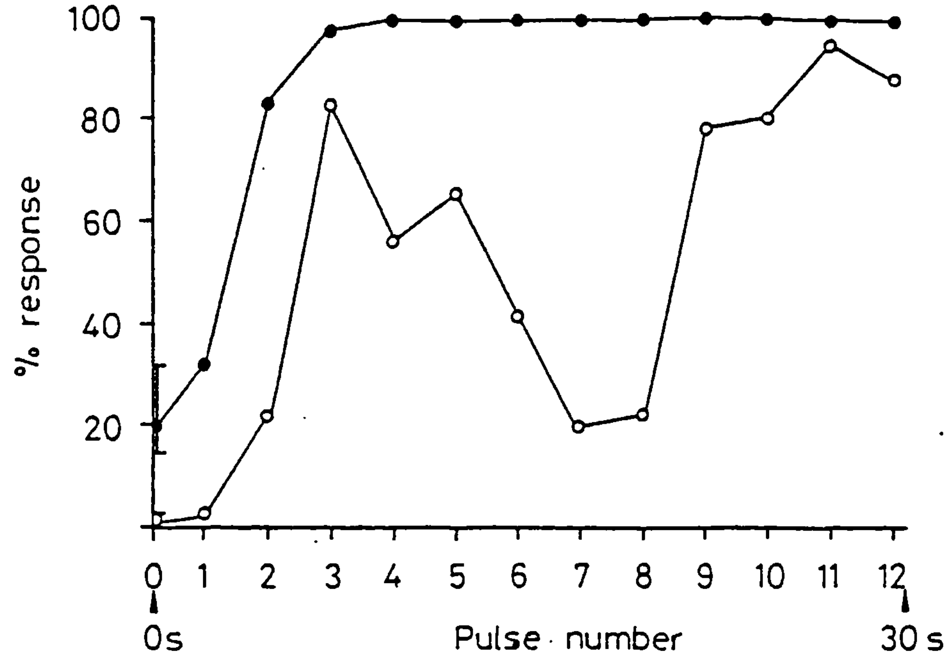


Figure 2.15. A conditioned response to a 30-s stimulus (on one trial) shown in terms of the numbers in Cage 1 (o) and aggregating at the feeding station (●) expressed as a percentage of the number of fish in the net (41). The point on Pulse 0 represents the 5 min pre-trial mean (± range).

NOTE: The percent response referred to in this figure and numbers 2.17, 2.19, 2.21, 2.25 and 2.26 refers to different numbers of fish than the percent response referred to during the small net experiments.

of view. The camera was calibrated by placing a ruler at known depths in front of the loudspeaker so that fish in different positions on the video monitor could be assigned to appropriate depth ranges. Using this technique there would have been a considerable variation in the apparent depths of fish at similar real depths but close to and at a distance from the camera. However, as the calibration was carried out in the centre of the area, around which the conditioned fish circled, the results provided a good indication of the depths utilised.

No approaches to the loudspeaker were seen during these observations and over 97% of the fish were observed within the top 40 cm of the water column (Figure 2.16). Using this technique, it was obvious that fish were aggregating around the ropes suspending the loudspeaker, although they were never very far from the feeding area. In fact, fish still aggregated around the ropes in the absence of the feeder and feeding square (Figure 2.17).

2.3.2.1.4. Results: pre- and post-trial behaviour

There was a significant increase in the mean pre-trial number in Cage 1 throughout the first 105 trials (tau = 0.144; n = 105; $p < 0.05$). There was still significant long term learning, however, even if the pre-trial mean on each trial was subtracted from the number in Cage 1 at the end of Pulse 4 of the conditioned stimulus (tau = 0.377; n = 103; $p < 0.01$).

On trials 114-116 the camera was placed in the centre of Cage 2, pointing vertically upwards from a depth of 3 m. A mean of 1.67 fish (range 0-3) were seen to be attracted to Cage 1 from Cage 3 in response to the 30-s conditioned stimulus on these occasions. These observations suggested that most fish had learnt to remain close to the border of Cage 1 and Cage 2 where there was some shelter provided by the scaffolding and associated fouling organisms. Further experiments (Sections 2.3.2.4., 2.3.2.5), however, showed that more than this number remained away from this area.

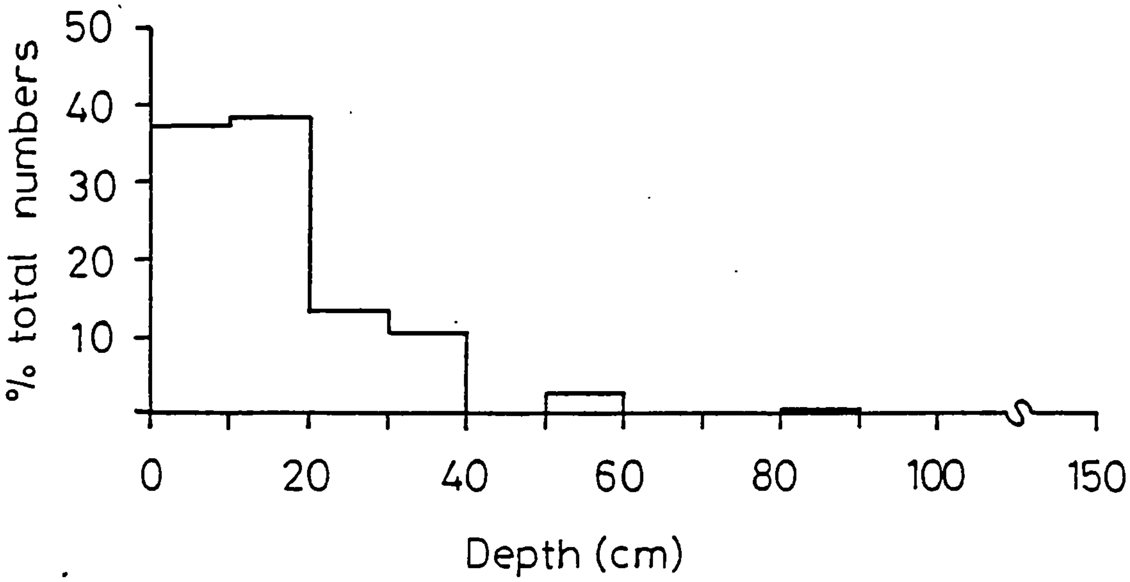


Figure 2.16. The depth distribution of fish responding to the conditioned stimulus. The data derive from 3 trials (107 - 109) during Experiment 5 (n = 538).

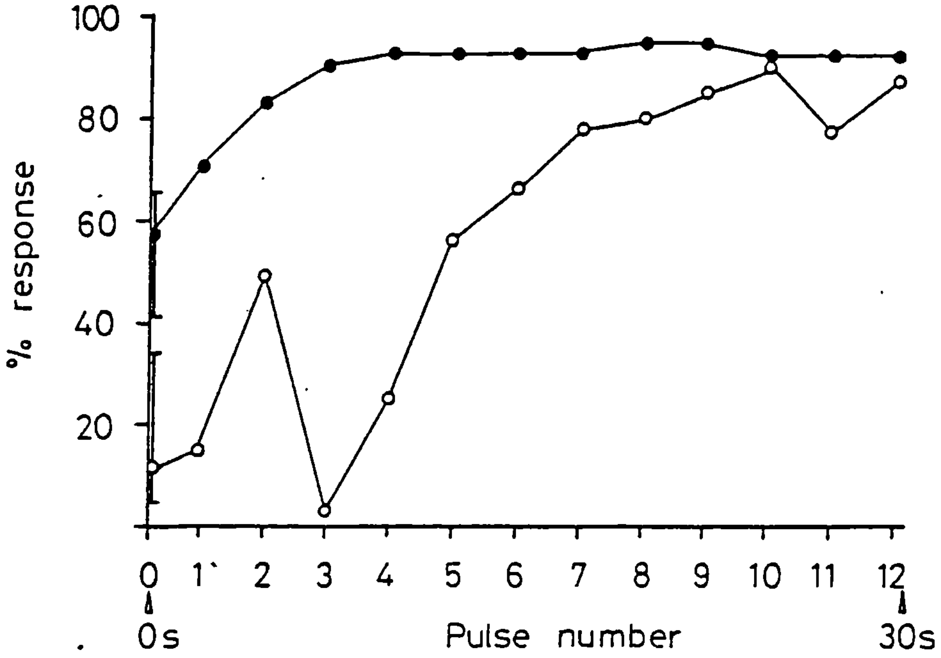


Figure 2.17. A conditioned response in the absence of the feeder and feeding square showing that aggregation occurs without these items. Response measured as the number within Cage 1 (●) and aggregating (o) expressed as a percentage of the number within the net (41). The data derive from one trial.Pulse 0 shows the 5-min pre-trial mean (± range).

In the first few trials fish took longer to move into, and remained in Cage 1 for a longer time than in later trials (Figure 2.18a and b). The faster decline in the numbers after trial 102 (Figure 2.18b) was both due to the fish having learnt that no more food was available and the aggression of a dominant individual in Cage 1.

2.3.2.1.5. Results: a comparison between the learning rates in the long and small net

The criteria used to judge conditioning in the small net experiments were the degree and consistency of aggregation around the feeding station expressed as a percentage of the total number counted feeding on each trial. In summary, during these experiments conditioning was complete, with a consistently greater than 75% response, after a maximum of 40 reinforced trials.

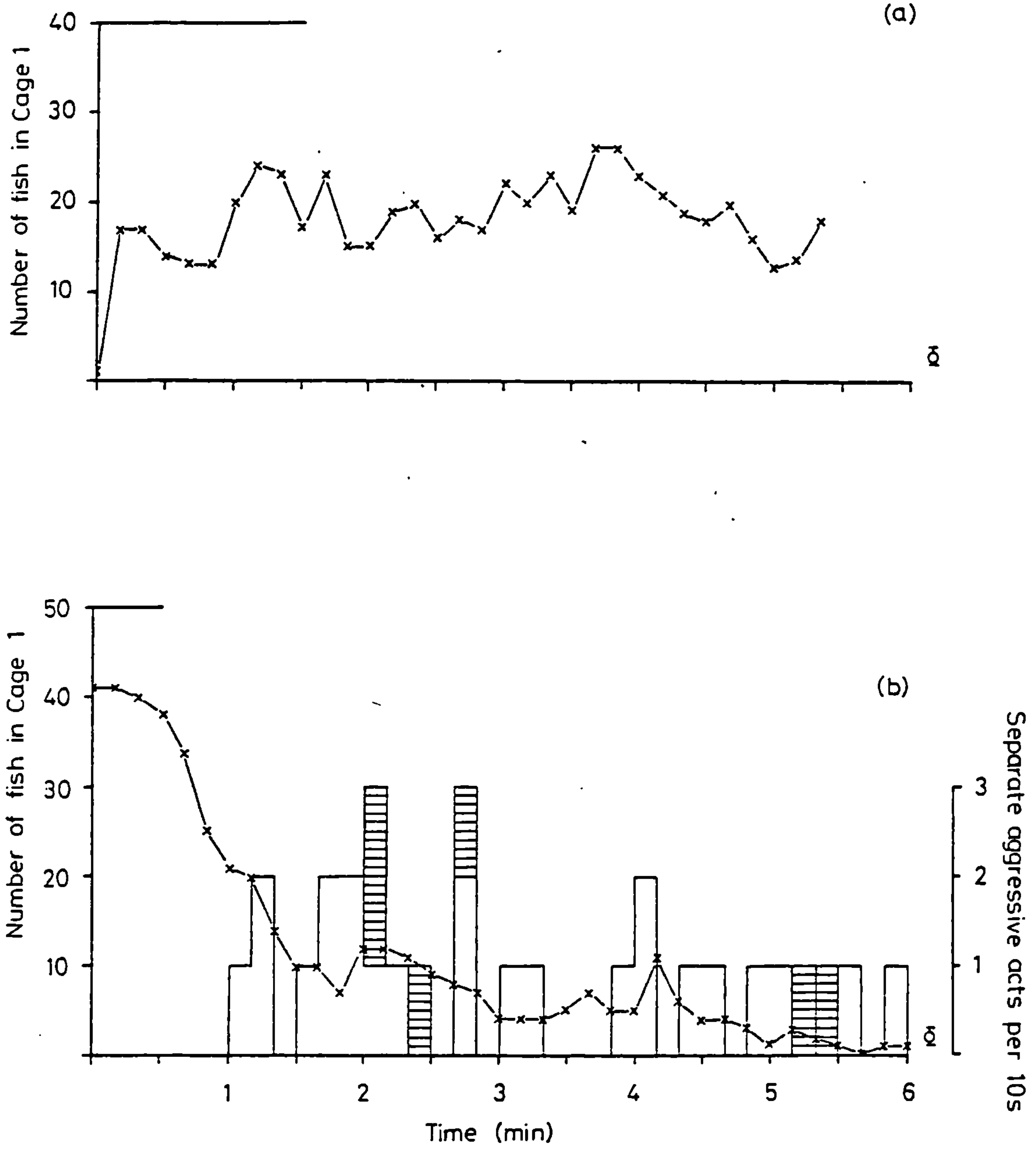
In comparison, in the long net consistently greater than 75% of the number feeding were attracted into Cage 1 by the conditioned stimulus (Figure 2.13) after 69 trials, although there was a significant increase in this percentage throughout the first 105 trials (tau = 0.564; n = 103; $p < 0.001$). Therefore, using this criterion of conditioning the learning rate was slower within the long net.

Because of the size of the long net the number feeding is also an important measure of the efficiency of the conditioned stimulus in attracting fish into Cage 1. A consistently greater than 75% response (% of total number in the net) in the long net was only reached after 86 trials, again suggesting a much slower learning rate under these experimental conditions.

If the degree of aggregation around the feeding station in the long net is compared with the results in the small net then the fact that this was inconsistent after 100 trials confirms that there was a large difference between the learning rates under the two experimental conditions.

Figure 2.18. A comparison of the numbers seen in Cage 1 post-feeding on trial 2 (a) and 102 (b). Horizontal bars indicate the approximate extent of feeding activity on each occasion. The separate point after 6 min shows the 5-min pre-trial mean (± range) for the following trial.

(b) also shows aggression by one dominant individual (□) and other fish (▤) in Cage 1 after feeding.


(a)
Number of fish in Cage 1
40
30
20
10
(b)
Number of fish in Cage 1
50
40
30
20
10
Separate aggressive acts per 10s
3
2
1
1
2
3
4
5
6
Time (min)

2.3.2.2. Aggression and territoriality

2.3.2.2.1. Territorial behaviour

After 52 trials, in Experiment 5, an individual was seen defending the area around the feeder against intrusion by other fish during the pre-trial period. This behaviour was more consistent after 71 trials when it was observed in 25 out of the following 34 pre-trial samples. Such behaviour was consistent with territorial defence with territory defined as "an area occupied more or less exclusively by one or more animals by active repulsion of potential intruders through defence or advertisement" (Keenleyside, 1979,after Wilson, 1975). This description is, however, not wholly descriptive of all the observed behaviour because territoriality broke down during the conditioned stimulus and feeding although it was resumed after feeding (Figure 2.18b).

The territorial fish was observed "charging" (Keenleyside and Yamamoto, 1962; McNicol and Noakes, 1981) by rapidly swimming towards intruders (termed "approach" by Jenkins, 1969). This behaviour usually elicited the immediate departure of the intruder but it was sometimes extended to "chasing" (Keenleyside and Yamamoto, 1962; McNicol and Noakes, 1981). Direct physical contact ("direct attack", Jenkins, 1969), occurred during some of these interactions. Behaviour interpreted as "lateral display" (Kalleberg, 1958; Hartman, 1965) was occasionally observed, although these and similar displays could have been missed as a result of the poor resolution of the camera system.

Territorial defence stopped during trials when other fish entered the feeding area en masse. Aggressive behaviour reappeared within one minute of feeding (although may have gone unnoticed before then) on trial 102 and was partly responsible for the decline in numbers in Cage 1 (Figure 2.18b). Fish were often chased out of the cage from the feeding area (distance > 2 m), with the pursuer following for all or part of this distance. The territorial fish was normally stationary below the feeding ring pre-trial, but was active over the whole of the feeding cage post-trial. Aggression was often directed towards fish closest to the feeding station, the result of which was a net movement of fish away from the proximity of the feeding area out, or to the peripheral areas of Cage 1, with the numbers dropping to pre-trial numbers in 5 to 6 min on trial 102. The territorial fish then resumed its pre-trial position near the feeding ring and so it was assumed to be the same individual as had been seen before the trial. It was never ascertained whether the same fish was involved in territorial defence over the long term.

2.3.2.2.2. Reaction of the dominant fish

The fish maintaining the territory around the only feeding point may or may not have been the same individual but must certainly have been one of the most dominant fish within the cage and therefore its reaction is of some interest. It was also relatively isolated from the rest of the group and so its reaction was less likely to have been influenced by other fish.

Using the terminology of Section 2.3.1.4., 63.2% of the observed initial reactions were positive and 36.8% were negative (n = 19). Of the subsequent behaviour, 47.5% were direct and 52.6% were indirect movements towards the feeding area. Fish close to the loudspeaker were more likely to show a negative, startle, reaction in the small net and so the high proportion of negative reactions is perhaps to be expected. No neutral reactions (which may be characteristic of less well trained individuals) were observed. Of the positive reactions, 83.3% resulted in a direct and 16.7% resulted in an indirect movement towards the feeding area. One was categorized as indirect because the fish was attracted to the surface reaction of another fish. Even when this fish reacted negatively, it was one of the first to enter the feeding area which suggests a high degree of "correct" responses. Even so, the results suggest that individual reaction types may not always be consistent in an obviously dominant fish, where its behaviour may also be modified by the behaviour of other fish and by the tendency to startle.

2.3.2.3. Transferred learning (Experiment 6)

2.3.2.3.1. Introduction

It has been suggested that the behaviour of individual fish may affect the responses of other individuals. It may, therefore, be possible to "seed" a naive group of fish with some conditioned individuals to accelerate the learning rate of naive fish or control their movements without any prior training. The aim of the present experiment was, therefore, to investigate whether there was any improvement in the learning rate or response of naive individuals when they were mixed with pre-conditioned individuals.

2.3.2.3.2. Methods

To a group of 39 individuals, conditioned for 152 reinforced trials in the first long net experiment, were added 164 experimentally naive fish of a similar size. All other experimental details were the same as before (Expt 5; Section 2.3.2.1.). Even though in Experiment 5 the 30-s signal initially improved the aggregation around the feeding station these pre-trained fish were conditioned to aggregate within 10 s and so the 10 s signal was again used to ensure that the results of Experiment 6 were comparable with those of Experiment 5.

2.3.2.3.3. Results: the conditioned response

The experiment was continued for 118 trials. The larger number of fish were very difficult to count accurately as a result of their tendency to overlap and group. This behaviour made it particularly difficult to count fish that were aggregated in Cage 1 at the start of the trial. These large numbers were usually recorded in Cage 1 after the first trial of the day after which fish tended to remain near to the feeding point. Thus, there was a significant increase in the 5-min pre-trial mean after the 0930 trial (Wilcoxon test; 0930 versus 1054 trial($T = 28$; $N = 19$; $p < 0.01$) although if all the trials were considered together there were no significant differences throughout the whole day (Friedman's two way analysis of variance; $\chi_r^2 = 5.541$; d.f. = 5; $p > 0.1$). There was also no significant increase in the pre-trial mean throughout the experiment (trials 1-118, tau = 0.097; $n = 105$; $p > 0.05$).

To compare the learning rate between Experiments 5 and 6 the numbers that were counted in Cage 1 at the end of the last pulse of the conditioned stimulus were expressed as a percentage of the number of fish that were removed from the net at the end of each experiment (Expt 5, 41; Expt 6, 194). Because the group of fish in Experiment 6 contained 39 pre-conditioned individuals the percent response was calculated as the total number responding less 39 as a percentage of 155 (194-39). The Wilcoxon test was then used to test the hypothesis that there was no significant difference between the two sets of data over the first 94 trials (no data for trials 95-105 in Expt 6).

There was a significant improvement in the conditioned response as a result of the inclusion of pre-conditioned individuals within the group ($T = 450$; $N = 85$; approximate normal deviate, $z = 6.034$; $p < 0.001$) (Figure 2.19). There was also considerably less variation in the numbers responding in Experiment 6 when compared to Experiment 5 although there was no significant difference in the mean percentage of naive fish feeding ($T = 1451$; $N = 83$; $z = 1.323$; $p > 0.1$) between the two experiments.

2.3.2.3.4. Results : aggregation around the feeding point

One measure of the degree of conditioning is the degree of aggregation around the feeding area. The numbers aggregating in the area around the feeding point (Section 2.3.2.1.2.) were counted in each trial and again, to facilitate a comparison with Experiment 5, this number was expressed as a percentage of the number of naive individuals within the cage (155). This analysis showed that there was no improvement in the aggregative response and

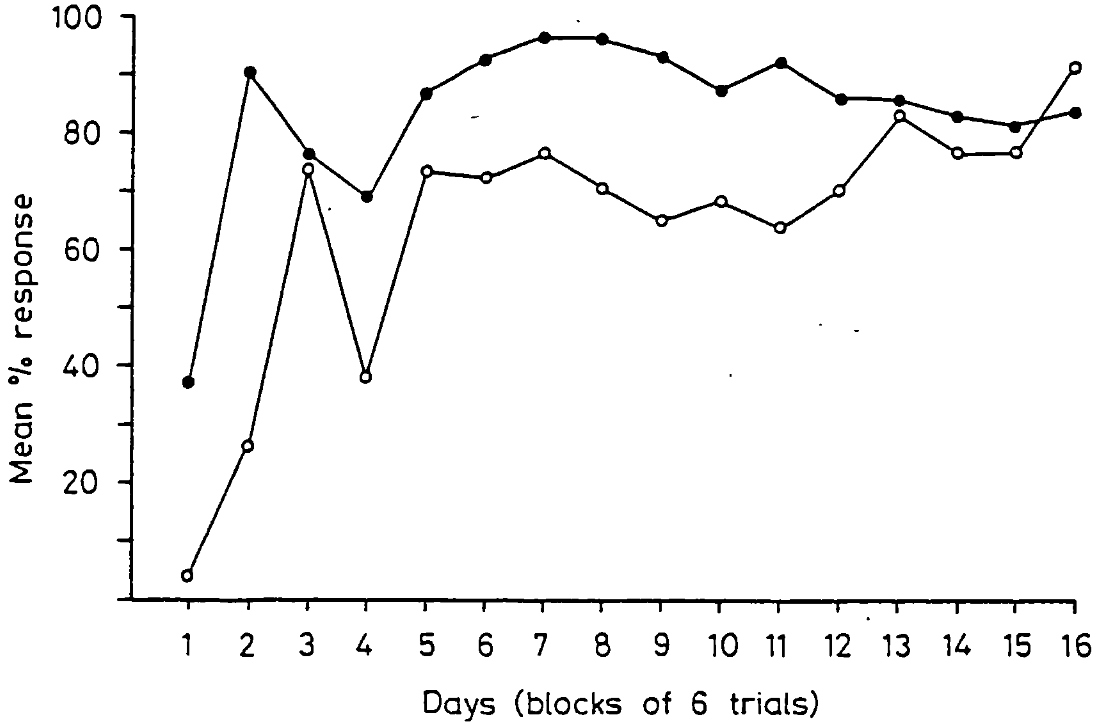


Figure 2.19. A comparison of the learning rate in the presence (●) and absence (o) of pre-conditioned fish. The response was measured as the number in Cage 1 at the end of Pulse 4 of the conditioned stimulus, expressed as a percentage of the number of fish removed from the net at the end of each experiment. (●, 194; o, 41). Each point represents the mean percent response for each day.

that fish in Experiment 5 were significantly more aggregated than those in Experiment 6 ($T = 130.5$; $N = 84$; $z = 7.376$; $p < 0.001$). This lack of improvement was not just due to the larger numbers being unable to aggregate in as small an area as those in Experiment 5 because less than 39 individuals were recorded on 61 occasions during 96 trials. It suggests rather that the pre-conditioned individuals were not behaving independently. Re-examination of the video tapes confirmed that this behaviour was again due to fish being attracted elsewhere in the cage by the unlocalized activity of other, probably less well trained fish, and is further evidence for the lack of independence of an individual within the group. The larger number of fish used during this experiment may have promoted greater disruptive activity.

2.3.2.4. Food only control experiments

2.3.2.4.1. Introduction and methods

To ensure that no extraneous cues were influencing the fish during Experiments 5 and 6, six trials were carried out with the loudspeaker disconnected at normal times (no 0930 trial) at the end of both of these experiments. All other experimental details were as normal.

2.3.2.4.2. Results

No reaction was observed to anything but the food during these trials, suggesting no extraneous cues were influencing the conditioned response.

The numbers counted feeding on these trials were significantly less than the mean of the normal trials (conditioned stimulus and food) either side (Wilcoxon test, $T = 0$; $N = 6$; $p < 0.05$). The mean difference in the number attracted with and without sound was 33.0% (range 7.32% -56.10%) of the number of fish within the cage (Expt 5, 41; Expt 6, 194). This result suggests that the sound signal was capable of attracting fish outside of the visual range of the feeder and there was, therefore, an advantage to using sound as a conditioned stimulus in the long net. Additionally, with the conditioned stimulus, more fish would have had better access to the food because they were required to aggregate close to the feeding point prior to feeding. This was not the case when only food was introduced because there was a greater time delay between the early and late arrivals.

2.3.2.5. Reaction to low amplitude signals

2.3.2.5.1. Introduction and methods

If the majority of fish tend to remain close to the feeding station they will always be exposed to a high amplitude conditioned stimulus. The series of experiments described in this section were conducted with conditioned fish at the end of Experiment 5 (after 128 trials) and Experiment 6 (after 118 trials) to examine the reaction of fish to lower than usual amplitude signals.

The ability of a fish to hear a sound signal depends on both the level of the stimulus and the background noise. During the following experiments, therefore, both signal level and ambient noise were measured at a depth of 1 m in between Cages 1 and 2 (2.7 m from the normal loudspeaker position, where fish usually gathered). At the end of Experiment 5 sound stimuli were generated from the normal loudspeaker position in Cage 1. After Experiment 6, the loudspeaker was placed at various distances outside the cage facing towards the main body and along the long axis of the net. In this latter case a dummy transducer was introduced into Cage 1 to maintain consistent visual cues.

2.3.2.5.2 Results

In both experiments there were no observable reactions below a sound pressure level of -1 dB//1μbar which corresponded to a minimum signal/noise ratio of 33 dB. This ratio is well above the threshold ratio of 23.75 dB, above which, according to Hawkins and Johnstone (1978), ambient noise (at 160 Hz)

Figure 2.20. The reaction of groups of rainbow trout to conditioned stimuli of varying amplitude expressed in terms of the signal : noise ratio.

(a) The effect of the signal : noise ratio on the conditioned response. The y- axis is the number in Cage 1 after a 9.5s (Line 1, Experiment 5) and 30s (Line 2, Experiment 6) conditioned stimulus minus the number in the field of view immediately pre-trial. To facilitate a comparison between the two experiments all points are expressed as a percentage of the number of fish removed from the cage at the end of each experiment (Experiment 5,41; Experiment 6,194) although the actual correlations were calculated using the actual numbers observed. Points marked with a - indicate that no reaction was observed. The correlations are:

Line 1 ; $r = 0.953$; d.f. = 4 ; $p < 0.005$

Line 2 ; $r = 0.861$; d.f. = 7;$p < 0.005$

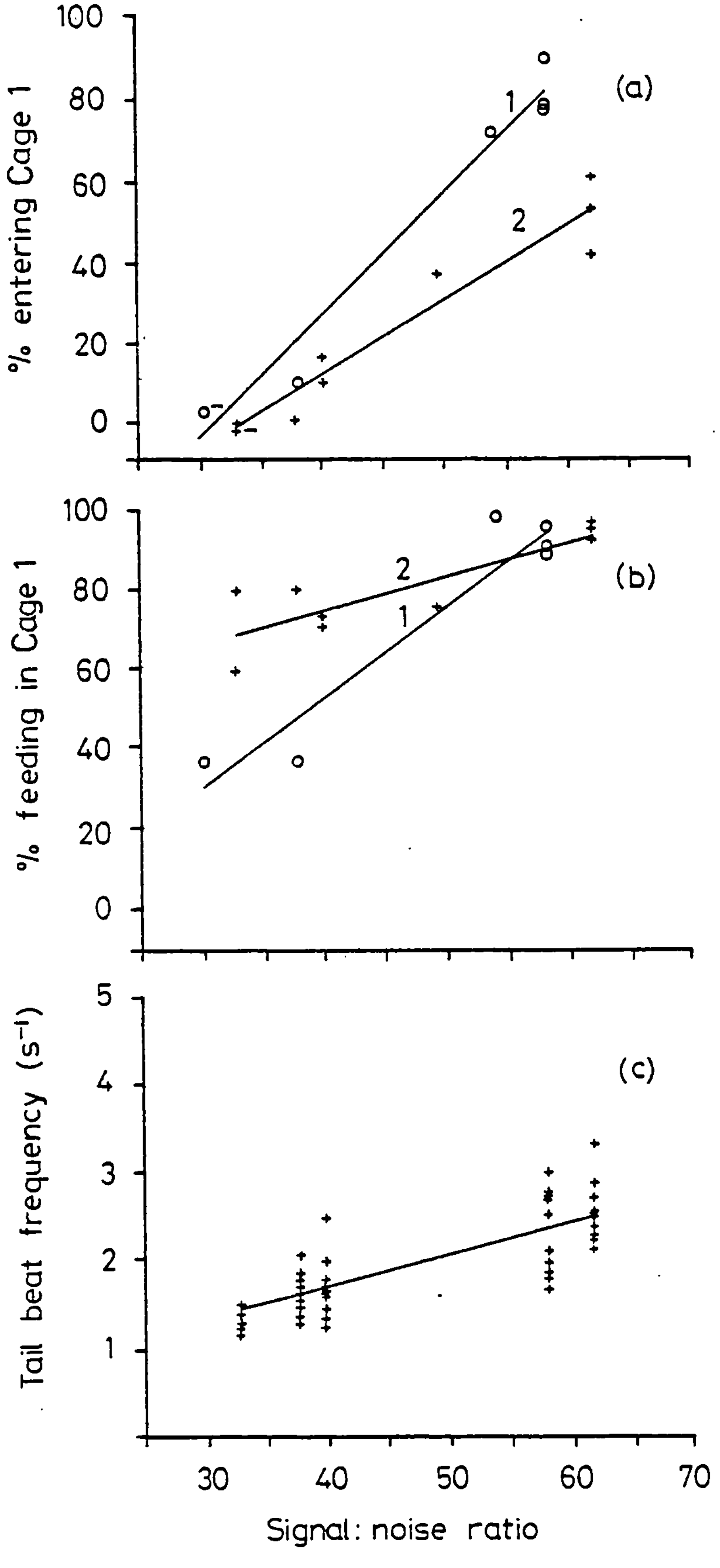
(b) The effect of the signal : noise ratio on the numbers feeding. The y- axis is the maximum number of fish feeding in Cage 1 in the 1 min post-feeding period. Percentages were used as in (a) with the correlations calculated using the actual numbers. The correlations are:

Line 1 ; $r = 0.938$; d.f. = 4 ; $p < 0.001$

Line 2 ; $r = 0.965$; d.f. = 7 ; $p < 0.001$

(c) The effect of the signal : noise ratio on the tail beat frequency of fish entering Cage 1. The data derive from Experiments 5 and 6. The correlation is:

$r = 0.777$; d.f. = 43 ; $p < 0.001$


% entering Cage 1
100
80
60
40
20
0
(a)
1
2
% feeding in Cage 1
100
80
60
40
20
0
(b)
2
1
Tail beat frequency (s⁻¹)
5
4
3
2
1
(c)
30
40
50
60
70
Signal: noise ratio

does not affect the hearing of the Atlantic salmon. In the present experiments, therefore, ambient noise probably had no effect on the thresholds. In both these and some preliminary experiments reactions were consistently recorded to levels greater than 0 dB//1μbar. In an experiment in the small net, conditioned fish reacted to a loudspeaker 21 m from the outside of the cage at a level of 0 dB//1 μbar (measured at 1 m just outside of the cage) so that, although it was difficult to quantify the position of the fish with respect to the signal amplitude, the threshold for the reaction lay at around 0 dB//1μbar.

In both Experiments 5 and 6 there was also a significant positive correlation between the signal/noise ratio and the number of fish moving into Cage 1 and the numbers feeding (Figure 2.20 a,b) suggesting that the greater the signal amplitude the further the fish were attracted to both the conditioned stimulus and food.

Fish reacted much less vigorously to lower amplitude signals. To quantify this reaction the mean tail beat frequency of the first 10 fish entering Cage 1 was measured over 4 or 5 cycles. There was a significant positive correlation between the signal to noise ratio and tail beat frequency (Figure 2.20c). This more vigorous response to the louder signals would also have been more attractive to other fish and helped to improve the numbers attracted to higher amplitude stimuli.

All reactions gave a net movement towards Cage 1, but aggregation was less consistent when the transducer was moved further away from the cage, suggesting that the sound field was important in mediating the response.

2.3.2.6. Reaction to sounds from different directions and the effect of visual cues

2.3.2.6.1. Introduction and methods

For a greater control of the movements of conditioned fish it is important that they can be attracted to sound sources in different positions. The following series of preliminary experiments examined the reaction of fish, previously conditioned to move to Cage 1, to sound stimuli originating from the opposite end of the net (Cage 4). Fish conditioned during Experiment 5, with 137 reinforced trials, were used for these trials. The feeder, feeding square, loudspeaker and camera were removed from Cage 1 and placed in the same configuration in the centre of Cage 4 leaving no obvious visual cues within Cage 1. Trials were then continued as normal.

2.3.2.6.2. Results

Initially there was a very poor response to the sound stimulus (Figure 2.21a), but it improved over the first day, especially when the signal was lengthened to 60 s on trial 4. The increase in the percent response was partly due to fish being attracted to and remaining close to Cage 4 as a result of food. On trial 11, an 0930 trial, no fish responded to the signal, suggesting that the fish had not learnt to move to the novel feeding station.

The visual and acoustic cues associated with the feeding station appeared to be operative at close range because on several trials a small number of fish aggregated close to the feeding station in Cage 4 in a similar way to the conditioned responses in Cage 1. The reasons for the inferior overall response, however, appeared to be that the fish were too well conditioned to responding in Cage 1. This interpretation was suggested by observations with the underwater television camera in Cage 2 (trials 7-9) and Cage 1 (trial 14).

Figure 2.21b shows the movement of fish throughout Cage 2 during trials 7-9. The pattern of movement was tested against the null hypothesis that there was no preferred direction. No significant difference was found in the pre-trial movements in the two directions ($\chi^2 = 0.60$; d.f.= 1; $p > 0.1$), although there was a significant net movement into Cage 1 in response to the sound signal ($\chi^2 = 10.89$; d.f. = 1; $p < 0.001$). Of the fish moving into Cage 1, 75% were observed swimming out of Cage 3 into Cage 1, and were thus swimming along a strong

Figure 2.21. The reaction of conditioned rainbow trout to the feeding station in a novel position in Cage 4 of the long net.

(a) The response as viewed with the camera in Cage 4. The number of fish in Cage 4 is expressed as a percentage of the total number removed (41) from the net at the end of the experiment. Arrows designate 0930 trials.

○ shows the number at the end of the 30-s conditioned stimulus

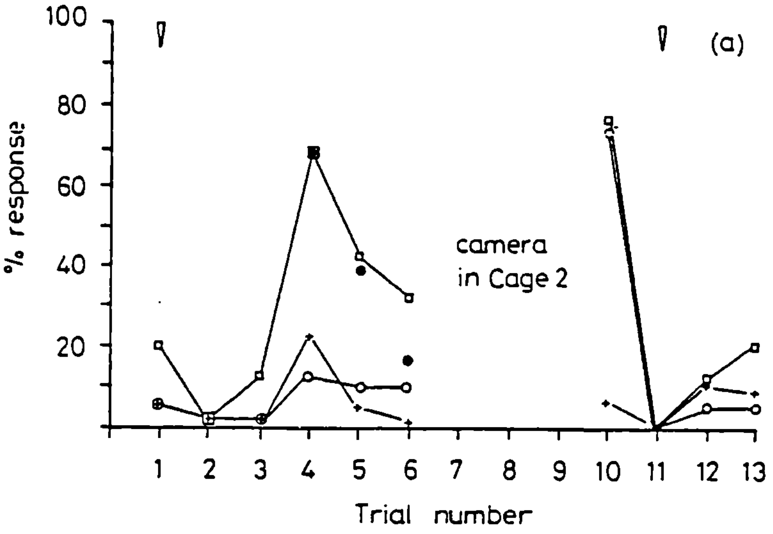
● shows the number at the end of the 60-s conditioned stimulus on trials 4-6

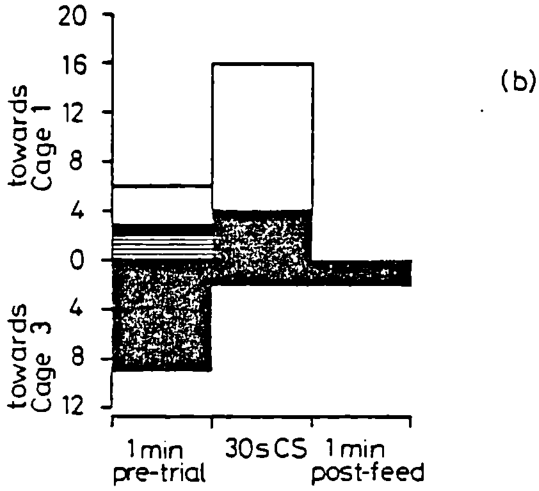
□ shows the maximum number seen feeding in the 1 min post-feeding period

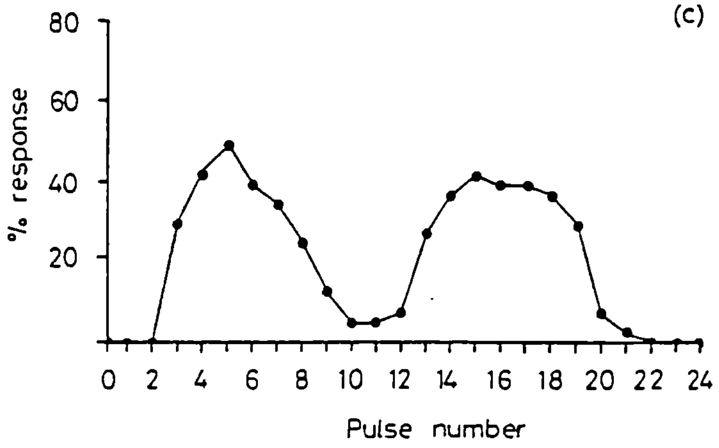
\+ shows the mean of the 5-min pre-trial period

(b) The response as viewed in Cage 2 on trials 7-9. The y axis represents the number of fish seen moving in the direction shown. These fish originated from Cage 3 (□), Cage 2 (▤) and Cage 1 (■). Those fish moving towards Cage 1 from Cage 1 moved out from and then back into this cage.

(c) The response as viewed in Cage 1 on trial 14, expressed as the number of fish seen in Cage 1 expressed as a percentage of the number (41) removed from the net at the end of the experiment.


(a)
% response
100
80
60
40
20
camera
in Cage 2
1
2
3
4
5
6
7
8
9
10
11
12
13
Trial number


(b)
towards Cage 1
towards Cage 3
20
16
12
8
4
0
4
8
12
1 min
pre-trial
30s CS
1 min
post-feed


(c)
% response
80
60
40
20
0
2
4
6
8
10
12
14
16
18
20
22
24
Pulse number

negative sound gradient where acoustic cues were being overridden by the visual cues associated with the cage environment. Despite the fact that a large number of fish were present in Cage 1, only two fish ever moved out of this cage when food was introduced into Cage 4. This result suggests that feeding cues were not transmitted between four cages within 1 min.

Observations in Cage 1 (Figure 2.21c) showed that even after 14 trials some fish were still overconditioned to moving into Cage 1 and apparently ignored the acoustic cues. As there was no apparatus in Cage 1, these responses must have been primarily due to conditioning to learned cues associated with the cage itself.

2.3.2.7. Directional hearing

2.3.2.7.1. Introduction

If rainbow trout are unable to localize the direction from which sound is coming, then this may limit their ability to detect the position of novel feeding points. Previous experiments (Section 2.3.1.5) suggested that rainbow trout could detect the direction of the sound within the small net. The next series of trials were carried out to investigate directional hearing over greater distances by examining the fishes' initial reaction to a more distant sound source.

2.3.2.7.2. Methods

After 120 trials in Cage 1 during Experiment 6 the reaction of the group to sounds coming from the loudspeaker within the main body of the cage at 2.0, 6.5 and 11.0 m from the edge of Cage 1 (3.75, 8.25 and 12.75 m from the centre of Cage 1) was observed with the camera in Cage 1. The sound pressure level at source was the same as before. The signal length was 10 s. To preclude visual orientation in the absence of a loudspeaker in Cage 1 a dummy was used in the normal position. The trials were not reinforced.

2.3.2.7.3. Results

Within this large group of fish it was very obvious that some individuals were reacting towards other fish. For example, when the main group of fish within the field of view of the camera reacted they disturbed the water surface and this resulted in an immediate turn by other fish towards the origin of this disturbance. This behaviour is more evidence of visual cues being used to mediate the initial reaction, but it made the interpretion of directional responses more difficult. Even so, the initial reactions could still be categorized into positive, neutral and negative reactions with respect to the 'normal' loudspeaker position. Using this categorization the effect of a change in the loudspeaker position on the number turning away from the 'normal' loudspeaker position was assessed. A significant increase in the proportion of "negative" (i.e. turns toward the live loudspeaker) reactions would suggest some directional hearing ability. To test for any significant change in the proportion of different reaction types the numbers in each reaction class on each 'novel' trial were compared with the numbers reacting in each class in the previous 'normal' trial using a 3 x 2 contingency table and calculating χ^2.

The results are shown in Table 2.11. There was no significant difference ($\chi^2 < 5.99$; d.f. = 2; $p > 0.05$) between the different proportions of reaction types observed on each novel trial, but there was some significant variation ($p < 0.05$) between normal trials which was probably due to a variation in the tendency to orientate to other fish. As all the responses to the novel positions were significantly different from all the normal responses the results suggest that the differences are due to the loudspeaker being positioned on the opposite side to normal and that rainbow trout have some directional hearing sense.

These results may also have been due to fish reacting to individuals closer to the transducer but outside of the field of view of the camera. Further experiments on the directional hearing ability of rainbow trout are therefore required before it can be unequivocally demonstrated. The present results,

Table 2.11. Initial reactions of fish in Cage 1 to sound stimuli originating from Cages 1,2,3 and 4. The distances given are the distances from the edge of Cage 1 to the transducer situated in the cage designated by the number in brackets. χ^2 compares the frequency of the three reaction types in the novel trial with the immediately preceeding normal trial. *, $p < 0.05$.

Position	n	Reaction type Positive	Neutral	Negative	χ^2
Normal (1)	1	18	17	14	
2.0 m (2)	1	5	19	22	9.16 *
Normal (1)	1	22	10	12	
6.5 m (3)	1	10	14	20	7.17 *
Normal (1)	1	19	26	18	
11.0 m (4)	1	11	11	27	8.39 *

NOTE: The χ^2 analysis is not validly applicable to these data.

together with those of Section 2.3.1.5., do suggest, however, that rainbow trout may have some directional hearing sense up to a distance of at least 11.0 m from this sound source.

2.3.2.8. Further training experiments

2.3.2.8.1. Introduction

In view of the importance of visual cues in mediating the conditioned response (Section 2.3.2.6), and the fact that this group of fish were to be released into the wild, it was essential to reinforce the acoustic cue as much as possible before liberating them. A series of trials were, therefore, started after this group had received 127 reinforced trials in Cage 1, first to reduce the importance of visual cues associated with Cage 1, and secondly to reinforce the acoustic cue by conditioning fish to move to a moveable sound source.

2.3.2.8.2. Methods

For the first 31 trials the "live" feeding station was placed in the centre of Cage 2. No other experimental apparatus was left in Cage 1. The camera was initially left in Cage 1, but was removed after 25 trials and in subsequent trials was moved around the four cages so that it would not be associated with any particular feeding point. The experimental and sampling protocol remained as before, except that the loudspeaker was suspended horizontally at a depth of 0.75 m pointing towards Cage 1 unless it was in Cage 1 when it faced the main body of the net. The shallower loudspeaker position was chosen for reasons that will be considered in the discussion. After initially conditioning fish to move out of Cage 1, the "live" feeding station was then moved around the net and a "dummy" feeding station, comprising a dummy loudspeaker, feeder and feeder ring was deployed in the centre of Cage 1. The sequence of configurations of the experimental apparatus is shown in Figures 2.22 and 2.23.

Figure 2.22. The response of fish to the feeding station in Cage 2 (trials 1-31).

● represents the "live" feeding station

■ represents the camera

- represents no data for that trial

Arrows and associated numbers indicate the net direction of movement and the accompanying χ^2 value associated with the null hypothesis that there was no net movement in either direction in response to the conditioned stimulus ($\chi^2_1 > 3.84$; $p < 0.05$).

The figure in the camera cage shows the number of fish in that cage at the end of Pulse 4 of the conditioned stimulus. Figures in brackets show the response at the end of Pulse 12 when an extended stimulus was used.

Time	Trial	Cage number 4	3	2	1	
				●		
1218	1			88·25 ▸	138	(a)
1342	2			87·75 ▸	133	
1506	3			0·02 ▸	15	
1630	4			60·14 ▸	129	
0930	5			16·82 ▸	86	
1054	6			19·38 ▸	113	
1218	7			128·81 ▸	192	
1342	8			—	—	
1506	9			34·39 ▸	75	
1630	10			55·93 ▸	110	
0930	11			26·52 ▸	0	
1054	12			41·38 ▸	127	
1218	13			1·95 ▸	53	
1342	14			62·44 ▸	112	
1506	15			69·34 ▸	75	
1630	16			28·94 ▸	95	
0930	17			24·72 ▸	1	
1054	18			21·32 ▸	80	
1218	19			35·5 ▸	130	
1342	20			13·01 ▸	95	
1506	21			1·41 ▸	44	
1630	22			0·40 ▸	5	
0930	23			26·33 ▸	18	
1054	24			5·30 ▸	64	
1218	25			—	—	
					■	

Time	Trial	Cage number 4	3	2	1	
				●		
1342	26		30 78 ▸	108	◂ 74·50	(b)
1630	27		0·26 ▸	117	◂ 96 40	
1755	28		0 0	78	◂ 44·84	
0930	29		31 69 ▸	80	◂ 109 64	
1054	30		0.0	60	◂ 46.29	
			(11 51 ▸	(132)	◂ 45 80)	
1218	31		0 21 ▸	90	◂ 67 84	
			(12 68 ▸	(199)	◂ 69 75)	
				■		

2.3.2.8.3. Results : feeding station in Cage 2; trials 1-31

The aim of this series of trials was to break the connection with Cage 1 and condition fish to move to the "live" feeding station in Cage 2. The results of these trials are shown in Figure 2.22.

Up to trial 20 there was an almost consistent significant movement of fish into Cage 1 in response to the conditioned stimulus (Figure 2.22). This initial behaviour was in marked contrast to the response to the novel position in the small net where fish at least moved towards the novel loudpseaker position. After trial 22 there was a consistent significant movement out of Cage 1. During the first 25 trials, with the camera in Cage 1, there was no significant change in the pre-trial mean (tau = 0.036; n = 23; $p > 0.10$), a significant decrease in the number of fish that were counted in Cage 1 at the end of Pulse 4 of the conditioned stimulus (tau = -0.352; n = 23; $p < 0.05$) and 5 s after the food had been introduced (tau = -0.628; n = 23; $p < 0.001$). Thus, although some fish were still conditioned to move into Cage 1 during this period, there was a decrease in the numbers doing it and an increase in the speed at which fish left Cage 1 when food was offered in Cage 2. This latter result was probably due to an increase in the number of fish feeding in Cage 2 immediately after food was introduced.

After trial 25 the camera was repositioned in Cage 2. This new position revealed an influx of fish from Cage 1 and Cage 3, but also some efflux into Cage 3. Extending the length of the conditioned stimulus to 30 s on trial 30 increased the overall flux throughout Cages 1,2 and 3, but substantially improved the final aggregation around the feeding area. All subsequent trials, therefore, used a 30-s conditioned stimulus.

After 31 trials in Cage 2, two trials were carried out with the feeding station in the previously conditioned position in Cage 1. There was a significant flux into Cage 1 from both Cages 3 and 2 (Figure 2.23a) suggesting that there was no loss of the original response as a result of conditioning in Cage 2.

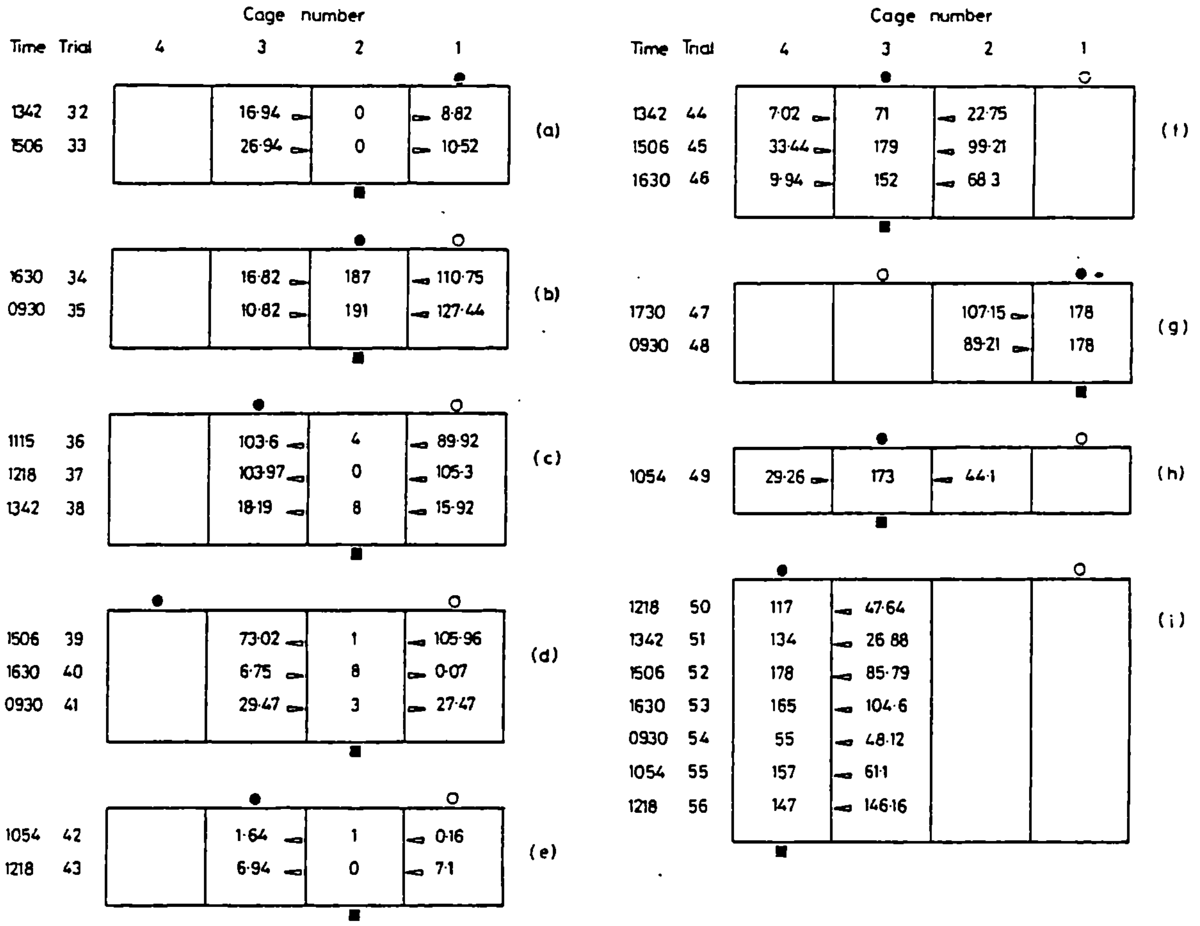
Figure 2.23. The response of fish to the varying configurations of the apparatus during the further training experiments (trials 32-56).

● represents the "live" feeding station

○ represents the "dummy" feeding station

□ represents the camera

Arrows and associated numbers indicate the net direction of movement and the accompanying χ^2 value associated with the null hypothesis that there was no net movement in either direction in response to the conditioned stimulus ($\chi_1^2 > 3.84$; $p < 0.05$). The figure in the camera cage shows the number of fish in that cage at the end of Pulse 12 of the conditioned stimulus.


Cage number
Time Trial 4 3 2 1
1342 32 16·94 0 8·82
1506 33 26·94 0 10·52
(a)
1630 34 16·82 187 110·75
0930 35 10·82 191 127·44
(b)
1115 36 103·6 4 89·92
1218 37 103·97 0 105·3
1342 38 18·19 8 15·92
(c)
1506 39 73·02 1 105·96
1630 40 6·75 8 0·07
0930 41 29·47 3 27·47
(d)
1054 42 1·64 1 0·16
1218 43 6·94 0 7·1
(e)
Cage number
Time Trial 4 3 2 1
1342 44 7·02 71 22·75
1506 45 33·44 179 99·21
1630 46 9·94 152 68·3
(f)
1730 47 107·15 178
0930 48 89·21 178
(g)
1054 49 29·26 173 44·1
(h)
1218 50 117 47·64
1342 51 134 26·88
1506 52 178 85·79
1630 53 165 104·6
0930 54 55 48·12
1054 55 157 61·1
1218 56 147 146·16
(i)

2.3.2.8.4. Results : feeding station in variable positions throughout the net; trials 34-56

Having broken the connection with Cage 1 the aim of subsequent experiments was to reinforce the acoustic cue and minimize as much as possible the importance of the visual cues associated with particular cages. The sequence of trials is shown in Figure 2.23.

Figures 2.23b and c show that, even with a dummy feeding station in Cage 1, the fish were able to respond to the acoustic stimuli in Cages 2 and 3. Trial 35 (Figure 2.23b) was carried out at 0930 suggesting that this response was a good learned response. In trials 36-38 a number of fish (mean 30; range 6-55), were observed to move out of Cage 1 only when food was introduced into Cage 3 showing not only that the visual stimuli associated with other feeding fish may be transmitted over three cages, but also that some fish were still not conditioned to travel three cages in response to the conditioned stimulus. Figure 2.23d shows that after 38 trials fish were still not conditioned well enough to be consistently attracted to the feeding station in Cage 4 although on trial 39 there was a significant movement towards Cage 4 from Cage 1 and Cage 2. The 0930 trial (trial 41) gave a very poor response, showing that fish were still overconditioned to Cage 1. On no occasion did fish appear to be immediately (< 1 min) attracted from Cage 1 to feed in Cage 4, again showing that visual or other cues associated with fish feeding in Cage 4 were not immediately transmitted over this distance.

The aim of trials 42-49 was to continue to reinforce the importance of the acoustic cue by conditioning fish to move between Cage 1 and Cage 3 (Figure 2.23 e-h). At the end of this series of trials, fish appeared to be well conditioned to move to the correct cage from any other cages although no 0930 trial was carried out. There was also no loss of the original response in Cage 1 (Figure 2.23g). These results suggested that at this stage most of the fish were able to use the acoustic cues to distinguish between "live" and "dummy" feeding stations.

The final trials (50-56) (Figure 2.23i) were designed to attract fish to Cage 4. It was evident from the results that not all fish were being consistently gathered to this end of the net. The mean percentage (of the total number of fish in the cage) that were attracted by the conditioned stimulus and food was 71.94% and 92.63% respectively. The 0930 trial (trial 54) gave a very poor result, suggesting further conditioning would be required to condition fish to move consistently to Cage 4. As the group had been satisfactorily conditioned to move at least between Cages 1 and 2 at 0930 and at least between 1 and 3 at other times, and time was short, the fish were considered ready for release into the wild (see Section 3).

2.3.2.8.5. Results : the swimming velocity of conditioned fish

The aim of this section was to determine how the swimming velocity changed during the course of the conditioned stimulus and feeding. Observations were made with the camera in Cage 2 and the "live" feeding station in Cage 3 on trial 43. Tail beat frequency was measured over 4 or 5 cycles near the centre of Cage 2 and used as an indirect measurement of velocity.

Throughout the course of the conditioned stimulus there was a significant increase in the tail beat velocity of fish moving across the centre of Cage 2 into Cage 3 (tau = 0.255; n = 76; $p < 0.01$) (Figure 2.24). The tail beat frequency of fish passing through Cage 2 to feed in Cage 3 was also significantly greater than it had been before feeding (Mann Whitney test; T = 200; $n_1 = 13$; $n_2 = 76$; $z = 4.487$; $p < 0.001$) showing that, although fish were increasingly excited throughout the course of the conditioned stimulus, probably as a result of more fish gathering near the feeding station, they were most attracted by the cues associated with food and other feeding fish.

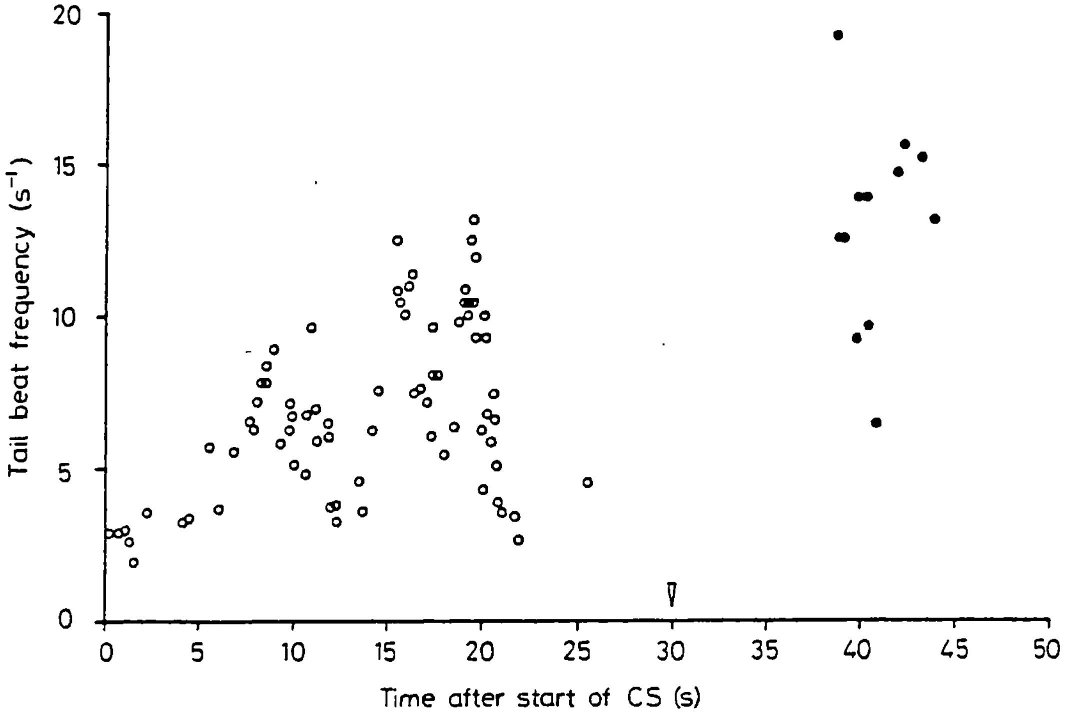


Figure 2.24. The tail beat frequency of fish moving towards Cage 3 in response to a 30-s conditioned stimulus and a food delivery in Cage 3. Arrow indicates the feeding time and the graph shows tail beat frequencies before (o) and after this time (●).

2.3.2.9. Generalization

2.3.2.9.1. Introduction

If a conditioned response has been established to one conditioned stimulus other similar stimuli may elicit a conditioned response. This phenomenon is known as generalization (Mackintosh, 1974). In the following experiments fish conditioned to 140 Hz in the long net during Experiment 5 were tested with stimuli of varying frequencies to investigate generalization in a group of conditioned rainbow trout.

2.3.2.9.2. Methods

Rainbow trout were exposed to stimuli six times per day at normal conditioning times. The only difference between these and training trials was that the frequency was different and no reinforcement was given. Frequencies were presented in a random order with an 140 Hz stimulus given on the 6th and 13th trial to record any decrement in performance.

The experiment was carried out with fish conditioned in the long net after 123 reinforced trials. A 30-s signal was used in these trials because this resulted in more consistent aggregation around the feeding area. The following stimulus frequencies were tested starting at 0930 and in the following order; 200, 100, 250, 350, 500, 140, 50, 120, 400, 380, 160, 300 and 140 Hz. The conditioned response was measured by counting the number of fish in Cage 1 and aggregating in a 1.20 x 1.20 m surface area centred on the middle of the loudspeaker at the end of Pulse 12 of the conditioned stimulus.

2.3.2.9.3. Results

Rainbow trout generalized and showed good conditioned responses to signals with frequencies of between 50 and 350 Hz (Figure 2.25). At 380 Hz a slight reaction was recorded (Figure 2.26) although this resulted in poor aggregation and the fish eventually lost interest and moved back out of Cage 1 before the end of the 30-s stimulus. This 380-Hz cut-off suggests that this is

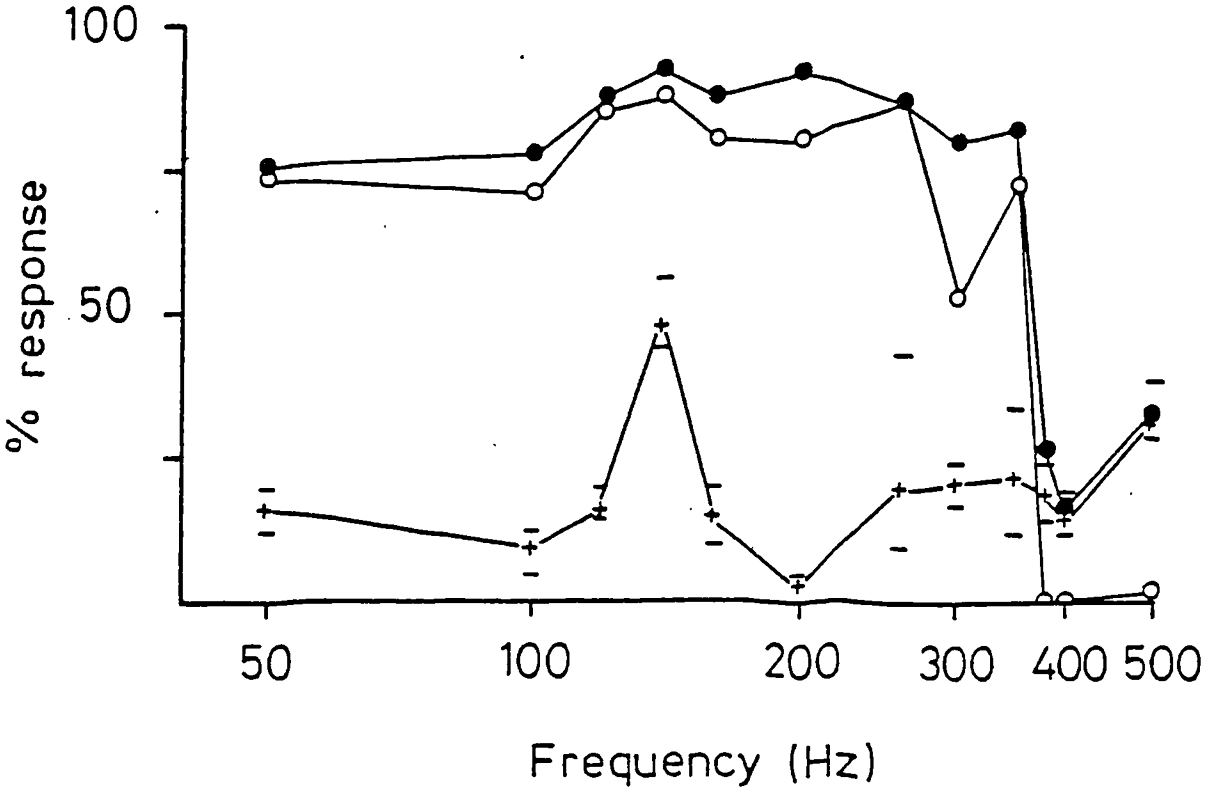


Figure 2.25. Generalization in a group of rainbow trout pre-conditioned to an 140 Hz conditioned stimulus. Response measured as the number of fish in Cage 1 (●) and aggregating at the feeding station (o) at the end of Pulse 12 of the conditioned stimulus expressed as a percentage of the number of fish in the net (41).

+ shows the 5-min pre-trial mean (± range) in Cage 1.

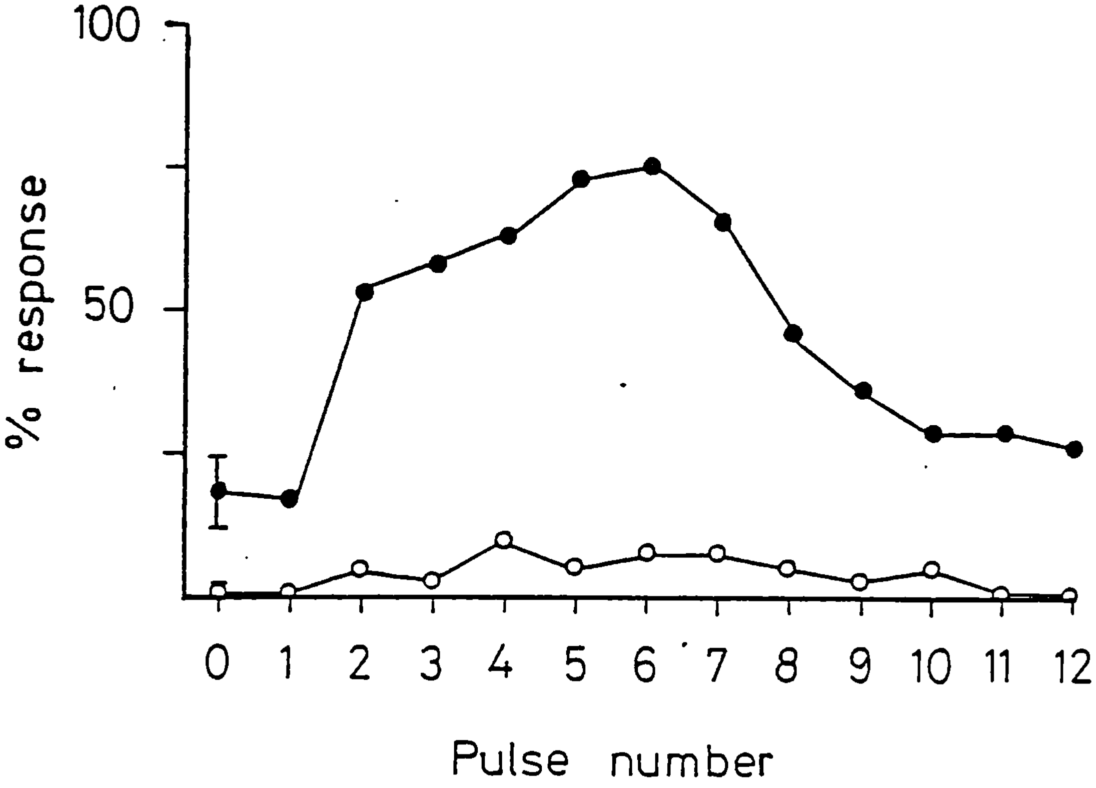


Figure 2.26. Generalization to a 380 Hz sound signal. Response measured as the number of fish in Cage 1 (•) and aggregating at the feeding station (o) at the end of each of each pulse of the sound signal. The count for Pulse 0 shows the 5-min pre-trial mean (± range).

the maximum audible frequency for rainbow trout under these experimental conditions.

2.3.2.10. The effect of benzocaine

2.3.2.10.1. Introduction and methods

Benzocaine (ethyl -p- aminobenzoate) (Laird and Oswald, 1975; Taylor and Solomon, 1979) was used to anaesthetize pre-conditioned fish for length/weight measurements and tagging. This experiment was designed to determine whether anaesthesia had any effect on the retention of the conditioned response.

Benzocaine was dissolved in 95% ethyl alcohol at a concentration of 1g. 10ml^{-1} and then added to full strength sea water at a concentration of 25 mg. l^{-1}. Thirty-nine fish conditioned in the long net during Experiment 5 were then introduced into this solution. After 3 min these fish had lost their equilibrium and after a further 2 min the fish were removed from the solution and returned to the long net to recover for 24 h. Four trials were then carried out at normal times on the second day following anaesthesia starting at 0930.

2.3.2.10.2. Results

Fish both moved into Cage 1 and aggregated around the feeding station in response to a 30-s conditioned stimulus. Of the 39 fish in the net, 82.1% (range 74.3 - 94.9) and 74.4% (range 66.67 - 89.7) were counted in Cage 1 and aggregating around the feeding station at the end of the 30-s signal respectively. This result suggests that benzocaine had no effect on the performance of the conditioned response although an improved response could probably have been attained by allowing full recovery over a greater than 24-h period.

2.3.3. The propagation of sound in Dunstaffnage Bay

2.3.3.1. Introduction and methods

The aim of this section was to describe the acoustics of the experiments and discuss some of the factors which could modify the hearing ability of the rainbow trout in Dunstaffnage Bay.

Measurements of signal propagation were made both in the experimental cages and from a boat moving along a transect line for up to 100 m from the sound source. Measurements were made with the hydrophone at depths of 0.1 m and at 0.5 m intervals from 0.5 to 5 m with the transducer positioned horizontally at 0.75, 1.5 and 3.0 m. The sound pressure at source was identical throughout all of these measurements and experiments (41 dB //1 µbar at 1 m from the source at a depth of 3 m in 5 m of water). The measurements were taken over a mud bottom at different stages of the tidal cycle in water ranging from 3.5 m to 15 m deep.

2.3.3.2. The acoustics of the small net used in Experiments 1-4 (Section 2.3.1.)

The experimental arrangement used during these experiments is discussed in the Materials and Methods (Section 2.2.5.1.; Figure 2.1.). It is clear from the measurements (Figure 2.27) that at a 1 m depth the signal is well above the threshold for hearing of around 0 dB// 1µbar (Section 2.3.2.5.) throughout the cage and that the sound pressure amplitude is noticeably reduced near the surface. This phenomena occurs because pressure waves destructively interfere with one another at the water surface because there is a phase change in the pressure wave at this reflecting boundary. Although sound pressure declines, the components of particle motion tend to summate near the surface (Hawkins, 1973) and therefore a given sound pressure will be accompanied by large particle displacements. Because salmonids are more sensitive to particle

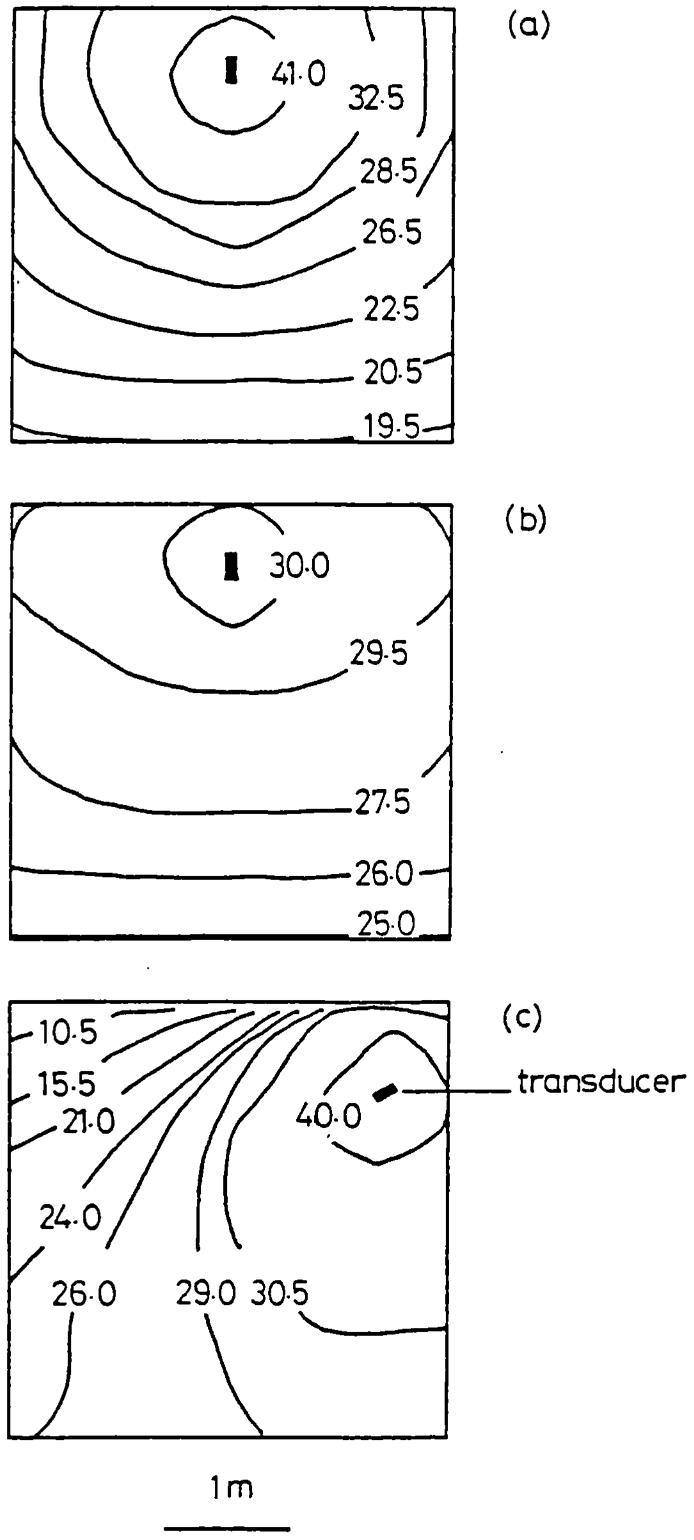
Figure 2.27. Sound pressure profiles through the small net used during Experiments 1-4.

(a) shows measurements taken on a horizontal plane with the hydrophone at a depth of 1 m.

(b) shows measurements taken on a horizontal plane with the hydrophone at a depth of 3 m.

(c) shows measurements taken on a vertical plane across the centre of the cage.

All sound pressures are expressed in dB// 1µbar.


(a)
41·0
32·5
28·5
26·5
22·5
20·5
19·5
(b)
30·0
29·5
27·5
26·0
25·0
(c)
10·5
15·5
21·0
24·0
26·0
29·0
30·5
40·0
transducer
1m

displacement (Hawkins and Johnstone, 1978) the conditioned stimulus would therefore have been very audible throughout the whole cage. Hearing would only have been masked when the spectrum level of ambient noise reached to within 23.75 dB (Hawkins and Johnstone, 1978) of the minimum signal level at 1 m of 19.5 dB// 1μbar. The ambient noise was unlikely to reach this required level of -4.25 dB// 1 μbar Hz^{-1} in Dunstaffnage Bay (Section 2.3.3.4.) and so there was probably no masking of the conditioned stimulus throughout any of the small net experiments.

2.3.3.3. The propagation of sound throughout the long net and Dunstaffnage Bay

Data from several sets of measurements in the long net and across other transects leading from the cages into deeper water were combined to produce regression equations describing sound propagation (Table 2.12). Only levels recorded at distances greater than 4 m from the transducer were used because there was a considerable variation closer to the source as a result of the differences in the loudspeaker depth.

There was no significant deviation from the spherical spreading law on any occasion (Table 2.12). The spherical spreading law assumes that sound propagates equally in all directions (Urick, 1975) but clearly this theoretical propagation cannot occur near a water/air interface which acts as an almost perfect reflector of the sound signal (Urick, 1975). In reality, the observed propagation is probably a complex summation of surface reflection and bottom absorption and without more detailed measurements does not warrant further discussion. A more detailed treatise on the subject of propagation in shallow water is, however, given by Albers (1965) Urick (1975), and Schuijf (1981).

At all loudspeaker depths the signal had to be greater than approximately 0 dB// 1μbar at 1 m to elicit a response (Section 2.3.2.5.). With the loudspeaker

Table 2.12. Regression equations describing the relationship between the sound pressure level and $\log_{10}$ of the distance from the sound source (d,m) in Dunstaffnage Bay. Each regression coefficient has been tested against the theoretical regression coefficient, β, assuming the null hypotheses that there is no change in level with distance (β = 0), cylindrical spreading (β = 10) and spherical spreading (β = 20). A significant t value signifies rejection of the appropriate null hypothesis.

***, $p < 0.001$; ** $p < 0.01$; *, $p < 0.05$; rest, $p > 0.05$.

Transducer depth (m)	Hydrophone depth (m)	n	Regression equation sound pressure =	t-values associated with the testing of different null hypotheses		
				β = 0	β = -10	β = -20
0.75	1	6	$27.90-22.68 \log_{10}d$	17.03***	9.52**	2.10
0.75	3	6	$35.15-21.70 \log_{10}d$	18.11***	9.75**	1.41
1.5	1	23	$25.82-18.97 \log_{10}d$	3.59***	6.43***	0.74
1.5	3	23	$35.02-19.61 \log_{10}d$	14.15***	6.94***	0.28
3.0	1	11	$28.83-17.58 \log_{10}d$	8.21***	3.54**	1.31
3.0	3	11	$39.02-19.03 \log_{10}d$	8.74***	4.14**	0.44

in its normal position in the long net it was approximately 15.0 m from the end of the net and at distances up to 16.0 m signals greater than 0 dB//1µbar were recorded on all occasions. Ambient noise never reached to within 23.75 dB of this level under experimental conditions (Section 2.3.3.4.) and thus, the signal would have been audible throughout the long net at all loudspeaker positions in all the experiments.

The deeper the transducer, the further the sound signal propagated (Table 2.12) and therefore, for a given transducer depth, the deeper a sound pressure receiver is, the greater the distance over which it can hear the sound signal (Table 2.13). Myrberg et al (1972) also showed that low frequency (f < 250 Hz) sound propagates least well near the surface. Even so, as sound pressure decreases near the surface and particle displacement amplitudes increase (Hawkins, 1973), the stimulation from particle motion, which is the relevant stimulus for salmonids (Hawkins and Johnstone, 1978), would be greater near the surface than appears from the consideration of sound pressure alone. To predict the audibility of signals with any greater accuracy it is therefore necessary in addition to monitor particle displacement amplitudes.

2.3.3.4. Ambient noise

Ambient noise was measured on the cages at a depth of 1 m on six separate occasions in conditions up to sea state 3 (Wenz, 1962). These conditions encompassed the majority of experimental conditions because the cage site was relatively sheltered from the prevailing westerly winds. The results (Figure 2.28) show that under these conditions the mean spectrum level of ambient noise is less than 23.75 dB below 0 dB// 1µbar and therefore masking would probably not have occurred in any of the nets. At sea state 3 a spectrum level of -30.5 dB// 1µbar /Hz was recorded and therefore, even under these more extreme conditions, masking would probably also not have occured. Wenz

Table 2.13. Transmission distances (m) ± 95% confidence limits to a sound pressure level of OdB//1 μbar calculated from the regressions given in Table 2.12. Confidence limits were calculated using the method described by Snedecor and Cochran (1978).

Depth of transducer (m)	Depth of receiver (m)	Transmission distance and 95% confidence limits (m) to OdB//1μbar
0.75	1	17.0 (11.9 - 24.2)
0.75	3	41.7 (29.7 - 58.6)
1.5	1	23.0 (11.51 - 45.8)
1.5	3	74.8 (31.3 - 119.1)
3.0	1	43.6 (19.6 -97.0)
3.0	3	110.5 (52.4 - 240.4)

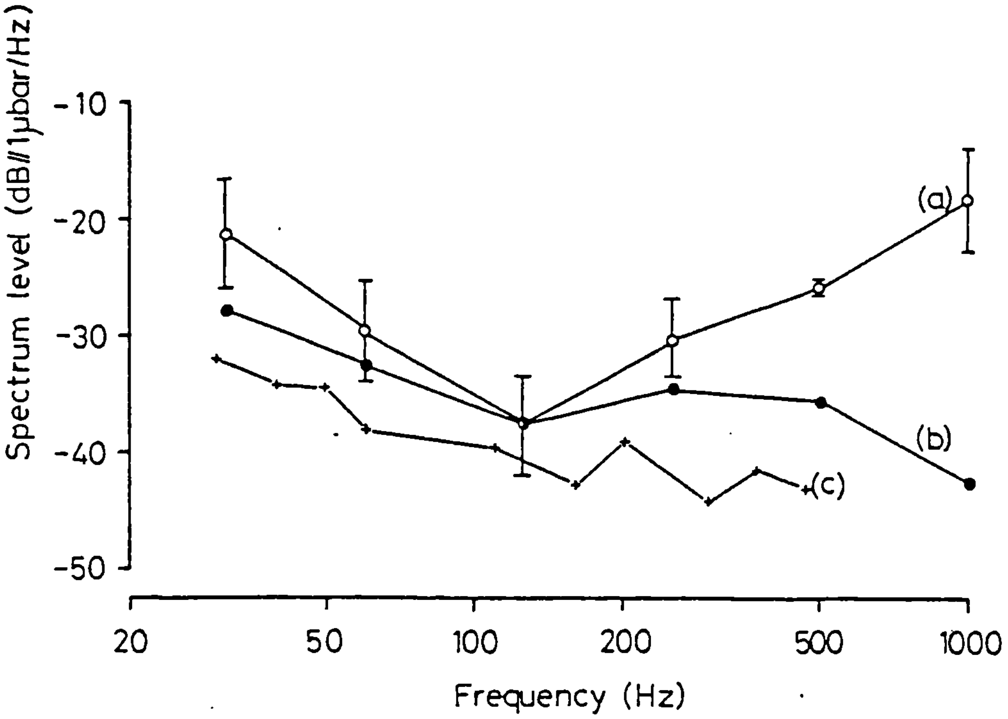


Figure 2.28. Ambient noise at the cage site in Dunstaffnage Bay and in Loch Torridon.

(a) Dunstaffnage Bay showing mean (± range) of measurements taken on 6 separate occasions in sea states 0-3.

(b) Dunstaffnage Bay with pump off at sea state 0.

(c) Loch Torridon in sea state 0, from Chapman and Hawkins (1973).

(1962) reports an approximately 20 dB variation in shallow water (< 200 m) ambient noise from sea state 0.5 to 7.0. Thus, even under the most severe conditions encountered in Dunstaffnage Bay audibility was unlikely to have been impaired in the small net. Hearing may, however, have been impaired under rougher conditions in the long net although these conditions were not encountered during this particular set of experiments.

The spectrum levels of ambient noise below 200 Hz agree well with the data of Chapman and Hawkins (1973) for Loch Torridon. Above 200 Hz there is some disparity between the two spectra which was primarily due to the operation of a submerged pump in Dunstaffnage Bay. When this pump was switched off, the ambient noise spectrum was similar to that observed in Loch Torridon (Figure 2.28,c).

2.4. DISCUSSION

2.4.1. The development of the conditioned response in the small net

Unconditioned rainbow trout were not attracted to the 140 Hz sound stimulus which agrees with the previous work with this species by Burner and Moore (1953, 1962). The results do show, however, that groups of rainbow trout are easily conditioned to aggregate at a feeding point in response to a sound signal. Although learning rates are only strictly comparable under identical experimental conditions (Mackintosh, 1974; Muntz, 1974) the rate of conditioning in the small net is comparable with other similar studies reported in the literature. For example, Abbott (1972) conditioned rainbow trout to aggregate around a feeding point in a 0.25 acre pond in 45 trials giving between one and four trials per day. Fujiya *et al.* (1974) conditioned red seabream, *Pagrus major*, to aggregate at a feeding point in response to a 200 Hz tone in 56 trials. Larson and Donaldson (1969) failed to condition fully a group of rainbow trout in a tank to an acoustic stimulus in 10 trials given at a rate of one per day.

Activity reached a variable plateau much earlier in the development of the conditioned response than the aggregative response. This difference is a typical result, as such activity responses, or preparatory conditioned responses (Mackintosh, 1974), generally condition more rapidly than more exact responses (Mackintosh, 1974).

The number of trials rather than the time over which they are spread appeared to be important in the learning of the present response. This result agrees with the observations of Dücker *et al.* (1979) who studied the significance of massed and distributed practice in discrimination learning by the goldfish, *Carassius auratus*, but, although they found no difference in the number of trials required to reach the criterion of conditioning, five trials per day combined with an even distribution of trials throughout the day were more efficient than 30 trials per day in accelerating the initial rate of learning. Pinckney (1966) showed that Mexican swordtails (Xiphophorus helleri) trained with an inter-trial interval of 20 min acquired an avoidance response quicker than fish trained with shorter intervals, although this training schedule is, of course, very different from that of the present study. Further shortening of the inter-trial interval in the present type of experiments could, however, decrease the learning rate particularly as care would have to be taken to maintain feeding motivation by not overfeeding and ensuring that enough food is introduced to provide some reinforcement for all of the fish within the group.

The development of the conditioned response was accompanied by a decrease in the proportion of fish reacting negatively and a concomitant increase in the proportion of positive reactions. McDonald (1922) and Moorhouse (1933) also reported a change from a fright reaction to a positive reaction in a similar appetitive conditioning experiment and Dill (1974) found that the flight distance of zebra danio (Brachydanio rerio) increased with prior experience of a predator.

The startle reaction, observed in fish close to the loudspeaker, is a typical salmonid reaction to high amplitude sound stimuli (Burner and Moore, 1953, 1962; Moore and Newman, 1962; Van Derwalker, 1967) and in the present study this stimulated other reactions in fish further from the sound source. This transmission of activity was probably mediated via the visual cues associated with the reacting fish because Verheijen (1956) found that a fright response to an alarm substance by Rasbora heteromorpha could be visually transferred to conspecifics that had not been exposed to the substance. The individuals further from the sound source must therefore have heard the sound above any startle reaction threshold. Also, because the proportion exhibiting negative reactions decreased during the development of the conditioned response most of the startled fish must have been reacting to the stimulus above any reflex or Mauthner mediated response threshold.

Rainbow trout do have Mauthner cells (Leghissa, 1942, in Eaton et al., 1977) which may mediate fast reflex responses with latencies, for initiation of the start of the response, of between 10 and 20 ms (Eaton et al., 1977, using vibrational stimuli; Webb, 1980, using electrical stimuli). Eaton et al. (1977) found that these reactions displaced fish between 0.5 and 1.5 body lengths from their initial position within 100 ms and so would have been discernable with the apparatus used during the present study. Thus, as the reaction times for negative reactions were usually greater than 100 ms, most were not Mauthner responses. The reaction times were of a similar order to those of Hunter (1969), Partridge and Pitcher (1980) and Partridge (1981) who found minimum latencies of 100 to 120 ms for visual responses to startle stimuli. Even so, the median negative reactions were significantly less than the other two reaction types and this may be, as Webb (1980) has suggested, that the reaction latencies to threatening stimuli are less than those to non-threatening stimuli. If this is the case then above any reflex reaction threshold the latency will depend on the significance of the stimulus. Therefore, the decrease in reaction time during the conditioning is to be expected and, indeed, is typical of an appetitive instrumental learning situation (Wolach et al., 1973; Mackintosh, 1974).

In a similar manner to the above, the increase in the proportion of fish moving directly towards the loudspeaker during conditioning is also to be expected. There was no evidence to suggest that fish learnt to aggregate directly below the feeding station, and indeed in other studies where the conditioned reinforcer is positioned close to the reward point it has also been found to become attractive (Mackintosh, 1974). Moorhouse (1933), however, found that surf perch, Cymatogaster aggregatus, in a tank initially aggregated near to the sound source but later learnt to aggregate at the feeding point although during his experiments the position of the sound source was occasionally changed and the sound and feeder were normally located on opposite sides of the tank. Therefore, if the feeder was placed on the opposite side of the cage in the present experiments fish would have learnt to aggregate below it, although the learning rate would probably have been slower under these circumstances (Moorhouse, 1933; Gallon, 1974).

There was an initial increase followed by a significant decline in the proportion of fish that were attracted to the feeding square. This behaviour may be interpreted in the light of the work of Mackintosh (1974) who suggested that the response that occurs at any stage depends on the unconditioned response at that stage. The unconditioned response to food was a movement towards the feeding square for food and an increase in activity; in fact both were observed. The decline in the former behaviour results from a shift in attention towards the conditioned reinforcer.

No reaction depth measurements were taken during these experiments but the fish were certainly aggregating near the surface (as judged by the splashing) and, like the long net experiments, were probably distributed in the top 0.60 m of the water column. This depth may represent a compromise between the surface feeding behaviour and the stimulus location, particularly as fish would have been stimulated to feed near the surface with the floating food.

2.4.2. Complications affecting the acquisition of the conditioned response in the small net

Group behaviour introduced considerable variability into the response. The variability was particularly noticeable before approximately trial 30 when fish were often attracted to the unlocalized activity of fish elsewhere in the cage. This unlocalized behaviour was probably attractive because it resembled feeding behaviour. Keenleyside (1955) has also shown how, even in the absence of food, the feeding postures of an individual may be attractive to other fish and such responses are likely to be well conditioned in a hatchery environment.

In addition, there was considerable variability introduced as a result of the serial aspect of the experiments. Agranoff and Davis (1968) and Shashoua (1973) found seasonal variations in the learning rate of goldfish related primarily to reproductive cycles. Hasler and Wisby (1951) also found differences in the retention of a conditioned response by two age groups of coho salmon. The primary differences in the present study were, however, probably due to variations in temperature although larger fish would have reached an apparently lower level of conditioning because they were not able to aggregate in as small an area as the smaller fish. Although rates of conditioning may be limited by the temperature (Prosser and Nagai, 1968), the primary effect of this variable in the present study would have been to act on the motivation to feed. At lower temperatures there is an increase in the residence time of food in the gut and hence a slower return of appetite which results in a lower motivation to feed (Grove _et al._, 1978). A decreased number of feeds per day may be more successfully used to condition fish at this time but, even so, fish took much longer to settle down in the experimental cage during the winter months and greater conditioning times should be expected. Wankowski (1981) also recorded a decrease in the responsiveness of starved Atlantic salmon parr to food when temperatures dropped during September.

Although fish may learn to anticipate feeding times if a constant feeding regime is used (Davis and Bardach, 1965; present study, Section 3.3.1.8.) there was no evidence of any significant increase in pre-trial activity during the course of these experiments. There was also no significant increase in the numbers aggregating in Sector 1 throughout the course of the experiments carried out at 6 trials per day. Landless (1974b) also found no significant aggregation with respect to the feeding point in small (< 1145 l) tanks although, as in the small net, the fish were within visible range of the feeder. There was, however, a significant increase in the pre-trial mean in Sector 1 during Experiment 3. It may be significant that this experiment was the longest in the series although, if learning depends on the number of trials, or food deliveries, and not the time over which they are spread, then the duration of the experiment should be of no consequence. The accidental dislodgement of pellets during raft maintenance and during windier conditions may have affected this result.

2.4.3. A comparison between the learning rates in the small and long net

Several variables which were not constant between the two sets of experiments were found to affect learning rates in the literature and may have been responsible for the variation between learning rate in these two experiments. These are discussed below.

In the long net, fish would have experienced lower amplitude stimuli than they had in the small net, both because of its size and, closer to the feeding station, because of the loudspeaker depth. A shallower loudspeaker generates greater particle displacement amplitudes near the surface, close to the source, than the deeper loudspeaker used in the long net. Therefore, because fish condition slower with lower amplitude conditioned stimuli (Mackintosh, 1974) one may have expected a slower rate in the long net.

Fish swam slower in response to lower amplitude stimuli and this behaviour could have resulted in the fish taking longer to reach the feeding station and adversely affected their reinforcement schedule. This slower response time is another common result of using lower amplitude stimuli. Woodward (1971), for example, demonstrated in Japanese carp (*Cyprinus carpio*) that a high conditioned stimulus intensity produced greater suppression of respiratory activity than a lower stimulus intensity.

Fish remaining close to the feeding point up to feeding time would have had their response reinforced immediately but fish further away in the long net would have experienced a delay between the end of the stimulus and the reward. An increase in this interval could also have promoted a slower learning rate (Mackintosh, 1974). Because not all the fish fed on each feed some individuals in the long net would have received only partial reinforcement which is also known to decrease the learning rate. If there was a consistent lack of reinforcement it could have resulted in the extinction of the response although the rate of extinction is less when splashing or other activity previously paired with the response is present (Salzinger et al., 1968). A more likely outcome was that individuals received different levels of reward. Goldfish trained to swim a runway for food swim faster when a large reward is offered than with a smaller reward (Wolach et al., 1973), so that the motivation of individual fish would have varied depending on the level of their reward and also the previous history of reinforcement (Mackintosh, 1971). Variations in the reward were probably related to the position of the fish in the net, but would also have been confounded by aggressive interactions.

The tendency to aggregate closer to the feeding station later in the experiment, which may have been enhanced by the use of a short 10-s stimulus, would, on the other hand, have improved the learning rate of the fish in the long net, both by exposing them to higher amplitude stimuli (see above) and by allowing more consistent reinforcement of the response. Abbott (1972) conditioned rainbow trout, in 45 trials, to move to a transducer for feeding in a 0.25 acre pond where some of the problems, arising from low amplitude stimuli, delayed and partial reinforcement would also have been operative. The major differences between the long net and Abbott's experiments were the loudspeaker depth and signal duration (0.30 m and 1 min respectively in Abbott, 1972) and therefore both of these variables were probably important determinants of the learning rate in the long net.

The location of the stimulus and reward affects the learning rate (Northmore, 1961; Muntz, 1974). Gallon (1974) found that goldfish learnt a shuttlebox avoidance task quicker and reached a higher asymptote of responding when the conditioned stimulus (light) was paired with the unconditioned stimulus (electric shock) than when these stimuli were at opposite ends of the box. In the small net fish closer to the feeding station would have been reinforced by swimming towards the transducer whereas those in the longer net would have swam above the loudspeaker and have had less directional acoustic cues and consequently have had to learn a greater number of visual orienting cues to mediate their response. The learning rate may therefore have been greater in the long net.

Further from the sound source the differences in position may not have been so important and indeed, because the signal propagates further from a deeper transducer, there is some advantage to placing it at this depth. The configuration of the conditioning apparatus may be most influential near the point of reinforcement, however, and consequently the depth may have been most important in determining the behaviour, and particularly aggregation, in Cage 1.

The inter-stimulus interval (ISI), the time between the onset of the sound signal and the food, is also an important variable which may have been responsible for some of the differences in learning rates between the long and small net and those of Abbott's. According to Mackintosh (1974) there is a general trend for an increase in the ISI to promote a decline in the effectiveness of the conditioned reinforcer. Although this trend may be true for laboratory studies, where the subject has easy access to the reward, it may not be in a field situation where it takes an appreciable time for the. subject to move to the point of reinforcement.

In the small net the 10-s stimulus allowed ample time for the fish to aggregate around the feeding station. In the long net the 10-s signal may have resulted in the lower number responding and given a false impression of the learning rate. To be counted as responding in Cage 1 a fish at the extreme far end of the net would have had to travel approximately 13 m at a mean velocity of 1.37 $m.s^{-1}$. This velocity corresponds to a tail beat frequency of 10.0 Hz for a 21-cm rainbow trout (Bainbridge, 1958) and is outwith the range of frequencies recorded in Cage 2 during the first 9.5 s of the conditioned stimulus (mean = 4.37; range 1.95 - 8.33; n = 17). In addition, because fish swam slower in response to low amplitude stimuli, fish at this distance from the source were unlikely to have been recorded as responding, although the reaction to low amplitude stimuli at the end of the net may have been different from those in Cage 1 where the reactions to these quieter stimuli were observed. Because fish may not have been able to reach Cage 1 before feeding this may have given rise to a delay, or even lack of reinforcement, which, as previously discussed, would have decreased the learning rate.

Although some variation in the response can be explained by fish being unable to reach Cage 1 in 9.5 s the differences in the number feeding at 0930 cannot be explained away in a similar manner. Fish were able to locate other feeding fish from two to three cages away and therefore an individual at the far end would have had to travel a maximum of approximately 8.5 m to be counted as feeding; an average velocity of 0.85 ms^{-1} over a 10-s period. This value represents a tail beat frequency of 6.7 Hz (Bainbridge, 1958) which is within the range of values observed in Cage 2. Even so, an extra short pulse (0.4 s) was given during feeding and fish did not stop during the sound-off interval of the pulsed signal and so were unlikely to have stopped at the end of the 10.4-s signal. Thus, the variation in the number feeding reflects a genuine lack of conditioning as well as a variation in the distribution of fish within the net. In future applications, however, a longer signal should be used to allow ample time to respond and may even improve the degree of aggregation.

The long net provided more opportunity for fish to stray from the feeding area and was therefore more like a field situation. It was, however, not surprising to find that fish eventually remained below the border between Cage 1 and 2 where there was some shelter provided by scaffolding and associated fouling organisms. De Vore and White (1978) suggested that salmonids prefer shade where available and in this net there was an obvious advantage in remaining close to the feeding area.

The poor 0930 response appeared to be due to fish moving away from the immediate vicinity of the feeding area overnight, but was probably also affected by the tendency to aggregate nearer the feeding station. There may also have been an overnight decrement in the learning process although this was not detectable in the small net experiments. This decrement may occur, however, as Mackintosh (1971) observed that the outcome of one trial depends on the outcome of several previous trials but less so when the trials are separated by an overnight break in the experiment.

2.4.4. Aggression and territoriality in the long net

There was a significant difference in the time fish spent close to the feeding point between earlier and later trials. Initially fish may continue searching for food in the area where food has recently been presented ("area-restricted searching", Thomas, 1974) and other fish may also have been attracted to the area after feeding. Although fish fed quicker in the later trials, because more individuals were in the cage when food was introduced, fish also left the cage much quicker on these occasions. Aggression was partly responsible for this post-feeding movement although, because some fish left before any aggression was observed, they may have learnt that no more food was available. These fish were less likely to be involved in aggression around the feeder, which may have been energetically rewarding, although their behaviour out of Cage 1 was not observed and they may have adopted territories elsewhere in the cage which they quickly returned to after feeding.

Salmonid feeding territories are economically defensible resources (McNicol and Noakes, 1981). The "charging" and particularly "chasing" observed in this study are the energetically most costly types of aggressive behaviour (McNicol and Noakes, 1981) making it important that the territory holder benefits in terms of increased food consumption (Davies, 1978; Rubenstein, 1981). Territoriality was abandoned, as fish moved into the cage prior to and during feeding, when presumably the costs of repelling intruders exceeded any energetic gain from exclusive use of the feeding area. Landless (1974b) also recorded similar territorial breakdowns during feeding in tank held rainbow trout. Unless food was accidentally dislodged from the feeder at other times however, because there would be no net food gain, there should be no advantage in being territorial.

The dominant fish could be better conditioned and remain close to the feeding point during the trial and so have better access to the food but, more particularly, it may gain better access to food through intimidation during feeding. Aggression was not observed during feeding but has been recorded in brown trout (Brown, 1946) and other species (Rubenstein, 1981). Changes in eye colour and body colouration may also act as non-aggressive reinforcers of a previously established dominance hierarchy (Keenleyside and Yamamoto, 1962) which may allow the dominant fish to be recognized (individual recognition has been recorded in several non-salmonid species, Myrberg, 1980). If the dominant is seen to possess a territory around the primary feeding site this ownership could reinforce its status and allow even greater access to food through intimidation of subordinates during feeding.

The aggression and territoriality could also have been innate and in this situation the dominant fish would have received no net food gain and the costs of territoriality would soon have outweighed the benefits. In such a situation, frequent changes in hierarchial position would be expected and would have gone unnoticed.

The presentation of food from a single feeding point would have promoted territoriality. For example, pygmy sunfish males, Elassoma evergladei, establish territories when prey are clumped and abandon it when prey are randomly dispersed at high and low densities (Rubenstein, 1981). Juvenile Atlantic salmon, Salmo salar, are also more aggressive in tanks with a single feeding point than with three (Wankowski and Thorpe, 1979).

The level and timing of food supply may also influence territoriality and aggression. Newman (1956) and Keenleyside and Yamamoto (1962) reported an increase in aggression following feeding to satiation, although Slaney and Northcote (1974) suggested that higher frequencies of aggressive interactions with low prey densities under more natural feeding conditions. Such effects may be complicated by the effect of food upon general activity (Keenleyside and Yamamoto, 1962), as feeding animals are more likely to encounter one another. The mere presence of food can also promote arousal (Kalleberg, 1958) and the sudden removal of food may promote aggression if "attack behaviour" is redirected from food to other fish (Newman, 1956). Although insufficient data were obtained there also appeared to be an increase in the number of aggressive acts in the present study after feeding which was probably primarily due to an increase in the number of intruders within the feeding area. The choice of an intruder to attack would have depended on its position within the dominant's territory and its length relative to the dominant as similar sized fish usually represent a greater threat (Wankowski and Thorpe, 1979). The distance at which an aggressive act is initiated also increases as the size difference between the two fish decreases (Dill, 1978).

2.4.5. The importance of vision in mediating the conditioned response

In both nets the visual cues associated with the environment were important in mediating the conditioned response. These cues were even shown to be important at the level of the initial reaction, although the position of the sound source was also important at this stage. Similarly, Hasler (1956) found that Phoxinus laevis used marks on the wall and floor of their tank to mediate a conditioned response. Aronson (1951) and Rasa (1969) have also shown that fish have a memory for topographic details which is important in homing and territoriality. Von Schiller (1949, in Thorpe, 1956) found that Gambusia affinis was unable to perform a maze task which it had learned in a small tank if the apparatus was put into a larger tank, suggesting that environmental visual stimuli were important in this learned response. Laboratory studies have shown that fish have good visual discrimination abilities (Northmore et al., 1978) and Adron et al. (1973) have shown that groups of rainbow trout can learn to discriminate the position of identical food acquisition triggers in a tank.

Because environmental cues were important in mediating the response it was difficult, particularly in the long net, to attract fish to other parts of the net. Olsen (1976) also found that saithe, Pollachius virens, conditioned to aggregate at a single feeding point in response to an 150 Hz tone would only move 10 m towards a novel feeding point 80 m away before returning to the original position. These saithe could be made to swim over these distances with additional training suggesting they were able to detect the acoustic stimuli but, like the rainbow trout, were "over-conditioned" to the original position.

The training technique used during the long net experiments probably confounded the "over-conditioning" problem. The rainbow trout could conceivably have been overconditioned as a result of the large number of trials in the long net. This possibility seems unlikely though because Abbott (1972) conditioned a group of rainbow trout in a 0.25 acre pond for 168 trials prior to successfully attracting them to another transducer 10 m away. A small number of fish did, however, remain near the original position, which probably represents the "over-conditioning" observed in the present study. The lack of response was also not due to signal length, although extending the length did result in some net improvement. The most likely variable influencing the relative importance of "overconditioning" was, therefore, the loudspeaker depth.

In the small net a shallower transducer was used and in Abbott's experiment the transducer was suspended at a depth of 0.3 m. With these shallower loudspeaker positions, as has been discussed, fish would have been continually reinforced by moving towards the source along a gradient of sound particle displacement amplitude. Conversely, in the long net fish may have been required to learn more visual cues to mediate their response because they were swimming above the transducer. If this was the case, then fish conditioned with a shallower loudspeaker could be easier to attract with another sound source because they use fewer visual cues to mediate their conditioned response. This hypothesis needs testing.

2.4.6. The importance of other fish in mediating the conditioned response

The visual cues associated with other fish were also shown to be important in mediating the conditioned response. Salmonids are visual feeders (Wankowski, 1977) so that vision is probably of prime importance in the reaction of fish to one another. Vision is important in triggering a direct approach to other fish in a shoal (Keenleyside, 1955) although both the lateral line and olfactory senses are also important in the maintenance of normal shoaling behaviour (Pitcher, 1979).

Other individuals would have been particularly attracted to other fish in the group if their behaviour resembled feeding behaviour. Haubrick (1961) found that in groups of South African clawed frogs, Xenopus laevis, a feeding or searching type behaviour by one or two members initiated similar activity in other members of the group. Olla and Samet (1974) also showed how feeding in isolated striped mullet, Mugil cephalus, was facilated by viewing a feeding group of conspecifics. Keenleyside (1955) found that any behaviour resembling feeding, such as the head down posture in the stickleback, stimulates activity but that the stimulus of feeding fish is more attractive than that of non-feeding fish or food alone. This latter result confirms those found in the long net where the velocity of fish moving towards the feeding station was greatest when other fish were feeding at the feeder.

Apart from a general increase in the activity of the group resulting from a response to the excitation of a few fish, individuals may have used other fish to mediate their own responses. For example, fish moving directly to the loudspeaker would have provided a visual stimulus to mediate the reaction of other fish. Indeed, some fish moving indirectly to the loudspeaker were observed to do so only after other fish had aggregated at the feeding station and, in this case, the site of active fish could have provided a focal point for the attraction of possibly less well trained individuals. Thorpe (1956) refers to such behaviour as "local enhancement" and this may conceivably improve the learning rate of less well conditioned individuals within the group.

During Experiment 2 there were unexplained variations between the behaviour of fish in similar positions. These variations may have arisen from differences between individual learning rates and motivation which could have been derived from differences in the social status of individuals within the group.

Yamagishi et al. (1978) found that the dominant fish within a group of four swordtails, Xiphophorus helleri, conditioned quicker than its three subordinates in a task of swimming to a feeding point in response to an 800 Hz tone. Subordinates were chased from the feeding point and allowed minimal reinforcement and so, not surprisingly, exhibited a poorer learning rate when tested individually. When the initially dominant fish was defeated and replaced by an initially subordinate fish, however, the former did not respond to the sound stimulus. The interaction between the lack of reinforcement as result of aggression and learning rate of a subordinate through being a subordinate per se makes interpretation of this study difficult. Intimidation during feeding may give rise to different levels of reinforcement, however, which effects the response rates (Wolach et al., 1973) and if subordinates receive less reinforcement they would then be expected to show poorer learning rates.

Landless (1974b) provides some supporting evidence for the social suppression of subordinate learning as he found that only dominant fish pressed the food releasing trigger within a group of demand fed rainbow trout. Milanovsky (1958, in Yamagishi et al., 1978) also found that socially dominant individuals within a group of pike, Esox lucius, conditioned more rapidly than subordinates. Thus, the better conditioned fish may be dominant and could certainly have helped mediate the responses of less well conditioned individuals. There is some classical evidence that dominant individuals lead groups of fish through mazes (Welty, 1934; Greenberg, 1947) although more recently Warren et al. (1975) could find no improvement in the avoidance response of a group of goldfish, Carassius auratus, after the inclusion of a pre-conditioned individual.

2.4.7. The transferred learning experiment; evidence illustrating the importance of other fish in mediating the conditioned response

Good supporting evidence for the importance of the visual stimuli associated with other fish was provided by the transferred learning experiment. In a similar experiment, O'Connel (1960) found that if a naive individual was introduced into a sardine (Sardinops caerulea) school this fish acted in perfect unison with a trained school from the first trial. Levin (1973, in Gleason et al., 1977) also reported that naive Rasbora heteromorpha separated from a conditioned school by a glass partition followed the trained group in a shuttlebox during the course of an avoidance task. Hale (1956) also found that if 'slow' (forebrain extirpated) green sunfish, Lepomis cyanellus, were mixed with normal 'fast' fish the slower fish increased in the rate of their reaction.

The improvement in response during the transferred learning experiment may have been due to contagious behaviour, the evidence for which has already been discussed and also local enhancement with the preconditioned fish attracting the naive fish into Cage 1. The results, however, conflict with Warren et al. (1975) who found no improvement in the response of a group of 9 naive goldfish after including one pre-conditioned individual within the group. The larger number of pre-conditioned fish used in the present experiments would have facilitated the response of the naive individuals and Sugita (1980) also found an improved response when a greater proportion of pre-conditioned fish were included in an group of naive guppies (Lebistes reticulatus). He also showed that these fish could learn an avoidance task if they were in the company of pre-conditioned individuals during unreinforced trials. Because his trials were unreinforced this behaviour is strongly suggestive of imitative learning. Sugita (1980) also found that naive guppies showed a greater tendency to follow pre-conditioned fish when they were given an electric shock which increased the cohesiveness of the group. This result suggests that animals, like rainbow trout, which form cohesive groups or other social groupings, are more likely to show such behaviour. Warren et al.'s and Sugita's studies used an avoidance conditioning paradigm but in an appetitive learning situation. the visual stimulus of pre-conditioned fish stimulated into a feeding type of behaviour would probably be more attractive to naive individuals. The result would be a considerable social facilitation of the feeding activity of other naive members of the group.

There was no evidence for an improved learning rate in the transferred learning experiment because the originally naive fish must be tested without pre-conditioned fish to demonstrate this. In the light of the data of Sugita (1980) some improvement may have been expected although, even if fish did not learn by observing the behaviour of other fish, there is considerable evidence that the presence of other fish per se improves the learning rates of groups when compared to isolated individuals. Welty (1934), Greenberg (1947), Anthouard (1972, in Warren et al., 1975, Beyer (1976)) and Munson et al. (1980) all found that groups learnt an appetitive instrumental learning task faster than individual fish and Hunter and Wisby (1964), Warren et al. (1975) and Gleason et al. (1977) report a similar enhanced learning rate for an avoidance task. The comparison is confounded because individuals isolated from a group may exhibit solitary inhibition (Clayton, 1978) and because fish trained in groups are often tested in groups. This objection may be overcome by testing all fish individually and Warren et al. (1975), who did this, found that goldfish conditioned in groups and tested individually performed better than individually trained isolates. Their results suggested that all members of the group acquired the task and that learning is enhanced as a result of the presence of other individuals per se rather than as a result of any leader/follower interactions. It seems highly likely though, in the light of the previous discussion, that learning must be modified by social relations within a group which Warren et al. (1975) were at pains to reduce.

2.4.8. The role of acoustic cues in mediating the conditioned response

The initial reaction of conditioned rainbow trout was also shown to be modified by directional acoustic cues and, because the fish appeared to be able to detect direction without moving, this result suggests that they were able to perceive enough information for localisation from one position rather than responding to graded intensity levels (e.g., Kleerekoper and Chagnon, 1954). These results do not imply that fish that did not react in a directional manner lacked any directional hearing capability. Such fish were probably orienting to other fish or visual cues associated with the cage environment.

Within the small net and close to the sound source the steep gradient of high amplitude particle displacements would have facilitated localisation via stimulation of both the lateral line (Van Bergeijk, 1964) and the labyrinths (Schuijf and Buwalda, 1980). Early experimenters (e.g., Von Frisch and Dijkgraaf, 1935) suggested that fish were only capable of directional hearing close to the source and Van Bergeijk (1964) proposed that acoustic localisation was only possible within the so-called 'near-field' (which extends 1.7 m from an 140 Hz sound source in the absence of reflecting boundaries) of the sound source where particle displacements exceed the thresholds for the lateral line detectors. These ideas have been superceded by a less restricted theory of localisation (Schuijf, 1981) and there is evidence, which is particularly extensive for the cod, Gadus morhua, that fish are capable of directional hearing outwith the 'near-field' and away from reflecting boundaries (reviewed by Schuijf and Buwalda, 1980). There is less evidence that fish are capable of directional hearing near the surface or in shallow water (Schuijf and Buwalda, 1980) where it may be more difficult because the directional stimulus of particle displacement is moving in a predominantly vertical plane (Banner, 1971). The present results are therefore of interest because there is both little information on directional hearing in salmonids and, in all species, little concerning localisation near the water surface.

The only data on directional hearing in salmonids is that of Abbott (1972) who, in one unrepeated trial, was able to attract ranbow trout to a novel feeding station 10 m from the original feeding point. The results of the present study suggest that rainbow trout may be able to discriminate between 180°

changes in the position of a loudspeaker at distances of up to 11 m from the sound source, although it was difficult to exclude orientation via the visual cues of other fish during these particular experiments. A more precise experiment was planned but, unfortunately had to be abandoned. In a shallow bay (< 3 m deep), Popper et al. (1973) found that two species of Hawaiian squirrel fishes (Mypristis spp.) were also able to respond to an 180° change in the direction from which pre-recorded alarm calls were transmitted at distances of up to 2 m. Olsen (1976) found that conditioned saithe, Pollachius virens, were able to choose correctly between sound sources at feeding points up to 80 m apart, although as Hawkins and Johnstone (1978) point out, the auditory capabilities of gadoids, such as saithe, are greater than those of salmonids.

After the fish reacted, directional acoustic stimuli as well as visual cues, would have modified its subsequent behaviour. The relative importance of the two cues probably varied with the state and method of conditioning. In the long net, for example, and before any additional training had been given, subsequent behaviour was found to be almost wholly mediated by visual cues associated with the cage. In the small net, the visual cues were less important as fish could aggregate, albeit not as well as normal, around a loudspeaker in a novel sector.

Kleerekoper and Chagnon (1954) found that conditioned Semotilus atromaculatus atromaculatus swam to the sound source in a tank along curved pathways and suggested that they located the source using gradients of intensity. The interpretation of these results is difficult because of the complex acoustic conditions prevailing in a small tank bounded by air (Parvalescu, 1967) although Richard (1968) suggested that free-swimming predatory teleosts located the position of an attractive sound source by exploratory swimming. Jacobs and Tavolga (1967) and Chapman and Johnstone (1974) have demonstrated that some fish can perceive amplitude changes and, although this ability remains undemonstrated in salmonids, it seems likely that the differences might have been used to modify subsequent behaviour.

The present results suggest that the auditory capabilities of rainbow trout are very similar to those of the Atlantic salmon described by Hawkins and Johnstone (1978). The generalization experiment showed that rainbow trout are capable of hearing stimuli between 50 and 380 Hz although the lower frequency limit was not determined. This restricted range compares well with that of the Atlantic salmon who are unable to hear frequencies above 380 Hz under field conditions (Hawkins and Johnstone, 1978). Stober (1969) reports a similar mean upper frequency limit of 443 Hz in cutthroat trout *Salmo clarki*, although this threshold was determined under laboratory conditions of high particle displacement stimulation where the upper frequency limit of Atlantic salmon may extend to 580 Hz (Hawkins and Johnstone 1978).

Comparison of thresholds is difficult because, as Hawkins and Johnstone (1978) point out, these can vary enormously depending on the way the sounds are presented. The difficulty in the present study was of measuring the relevant amplitude at the fish and this cannot really be done without restraining fish within a smaller area and measuring the particle displacement, as well as sound pressure, at the relevant position. In spite of this limitation the measured threshold of approximately 0 dB//1 µbar at 1 m depth was similar to that of the Atlantic salmon and above that of auditorally more specialized species such as cod (Chapmans and Hawkins, 1973) or the even more specialized ostariophysines (Hawkins, 1981). Depth measurements (Appendix A) showed that the fish usually aggregated above the 1 m deep hydrophone. Therefore, because particle motion increases as pressure decreases near the surface (Hawkins, 1973), the threshold would have been less if it was measured in terms of sound pressure nearer the surface (Hawkins and Johnstone, 1978).

2.4.9. Generalization

The present study showed that groups of rainbow trout trained at 140 Hz generalized to any other pure tone sound stimuli that they could hear. The upper limit at approximately 380 Hz represents the upper limit of the hearing range of salmonids in the field (Hawkins and Johnstone, 1978). Fujiya et al. (1974) reported a marked generalization decrement to an acoustic stimulus in the red sea bream, Pagrus major, which was not observed in the present study. Mackintosh (1974) has shown, however, that a number of variables may influence the degree of decrement and with rainbow trout the strong mutual stimulation effect would have helped to improve the response. The results do not, however, imply an inability to discriminate tones.

It may be argued that the small generalization decrement was a result of consistent transients in the sound signal, associated with the fast rise time and cut-off of the sound pulse. The strong cut-off at 380 Hz strongly suggests, however, that the pure tone frequency was the important stimulus. The small decrement suggests that the experimenter's change in frequency represented only a small part of the total experimental set-up reinforced during the trials (Mackintosh, 1974). Such an interpretation illustrates the importance of other visual stimuli, such as other fish and the environment, as suggested earlier. The temporal properties of the conditioned stimulus may also be more important to the fish than the frequency characterisitics and thus have contributed to the small decrement. Fay and Popper (1980) review the literature on acoustic communication and conclude that the temporal processing in many behavioural contexts may be more important that processing in the frequency domain.

The responses to low amplitude stimuli are an example of intensity generalization (Mackintosh, 1974), as there was a reduction in the magnitude of the response, both in terms of speed and total numbers, with a reduction in the sound pressure level.

2.4.10. Memory

There was no decrease in the performance over a 25 day period. The retention time is probably much greater than this because a trigger pressing response of rainbow trout can be retained for at least 3 (Adron et al., 1973) and 2 (Landless, 1974b) months. Stetter (1929, in Thorpe, 1956) found that Phoxinus had a memory for absolute tones of between 1 and 9 months. Red sea bream, Pagrus major, retained an acoustic reinforced response for at least 4 months (Fujiya et al., 1974). Such relatively simple tasks may last for even longer because Tarrant (1964) found that juvenile sockeye salmon, Oncorhynchus nerka, retained a light/food conditioning task for at least 374 days, although fish tested after 282 and 374 days showed a decrease in the vigour of the response and no response was discernable after 639 days. Tasks are probably retained in relation to their significance to the mode of life of any particular fish. Retention time may also vary with temperature (Stascheit, 1979).

2.4.11. The effect of anaesthesia

The physiological effects of anaesthesia have been well documented (McFarland, 1960; Wedemeyer, 1970; Soivio, et al., 1977; Taylor and Solomon, 1979). In the present study, handling and the use of benzocaine at a concentration of 25 $mg.l^{-1}$ had no adverse effect on the conditioned response. Fujiya et al. (1974) also found that "a tagging operation under anaesthesia" had no effect on the retention of an acoustic reinforced appetitive instrumental task. McNicholl and Mackay (1975) showed that treatment of rainbow trout with MS 222 at a concentration of 100 $mg.l^{-1}$ had no effect on the retention of an avoidance task over a 48-h period. Goddard et al. (1974), however, found initial behavioural changes in MS 222 (150 $mg.l^{-1}$) treated fish exposed to a temperature gradient. The latter suggested a week to recover from anaesthesia although the only limit in appetitive conditioning studies would appear to be due to the time taken to resume normal feeding behaviour. It seems unlikely though, that either MS 222 or benzocaine (a homologue of MS 222, Laird and Oswald, 1975) has any long term effect on the retention of a conditioned response.

SECTION 3

THE MOVEMENTS OF FREE-RANGING RAINBOW TROUT IN RELATION TO A FEEDING STATION

3.1. INTRODUCTION

The previous section was concerned with the conditioning of rainbow trout to sound in an enclosure. The present section concerns both the application of this technique in the field and, as a control measure, examines the relative effectiveness of a point food source without a sound stimulus.

Wilbur (1974, 1978) and Wilbur and Crumpton (1974) have found that a variety of freshwater species may be attracted to artificial shelter and supplementary feeding points. Fishelson (1980) also suggests that artificial shelter may be used to concentrate and increase the local productivity of some marine species. Similarly, aggregations of other marine species have been recorded around North Sea oil platforms (Olsen and Valdermasen, 1977) and artificial reefs (Yatomi et al., 1979), presumably in response to a local increase in the availability of food and shelter. Landless (1978) also showed that rainbow trout could be attracted to a supplementary feeding point in a small 8-acre loch. Randolph and Clemens (1976a,b), however, found that although channel catfish, Ictalurus punctatus, made daily excursions to a feeding point in a culture pond they occupied distinct home ranges away from the feeder at other times and that this routine was markedly affected by dominance/subordinate relationships and temperature. Thus, although some form of attraction is predictable when rainbow trout are released and a food source is added, there is little information on the development of this response to the feeding station, the distance over which they can be attracted and the factors affecting the attraction and distribution of this species around a supplementary feeding point. The first part of the present study therefore examines the relationship between an introduced stock of rainbow trout and a single supplementary feeding point in an 8-acre loch. This experiment served both as an experiment in the manipulation of movements with a point food source and as a control to the second part of the study where pre-conditioned fish were released and a pre-feeding sound stimulus used.

The literature on conditioning has been reviewed in the introduction to Section 2 although the work of Olsen (1976) and Balchen (1977a,b,c) who conditioned saithe, Pollachius virens, to move up to 80 m between feeding stations in response to a sound signal is particularly relevant to this section. This result may not, however, be applicable to rainbow trout because the auditory capabilities of salmonids are below those of gadoids such as saithe (Hawkins and Johnstone, 1978). In spite of this, Abbott (1972) was able to attract conditioned rainbow trout to a feeding station in a 0.25 acre pond using sound which suggests (although this information is not given) that this species could be attracted from up to approximately 30 m away. He also suggests that rainbow trout could be pre-conditioned prior to release into a larger body of water and thus, in the second part of this section, rainbow trout that had been pre-conditioned in cages in Dunstaffnage Bay were released into an 8-acre loch to determine both the effectiveness of pre-conditioning and the range over which they could be attracted.

3.2. MATERIALS AND METHODS

3.2.1. Experimental site

Experiments were performed in Loch Charn, an approximately 8-acre hill loch above Kilninver, near Oban (Figure 3.1). Loch Charn is an oligotrophic type loch (pH 6.95; alkalinity 12 mg Ca $CO_3.l^{-1}$), with a limited littoral zone shelving steeply close to the shore in all but the northern bay. The maximum depth is 16.6 m (Figure 3.1). The littoral zone is dominated by the common reed, Phragmites communis, and the white water lily, Nymphaea alba. Several small burns feed the loch, the largest of which is at the SSW corner. No fish could have emigrated through these burns during the study period because marshy ground barred any access from the loch. There is only one outlet in the NNE corner and it was possible that some rainbow trout may have left via this exit, although none were ever observed in this burn, despite several checks, and there were no reports of any tagged fish taken from outside the loch.

The loch was thermally stratified in both May 1981 and September 1981 so this would probably have been a feature of the loch throughout all of the experiments. A temperature record was kept (Figure 3.2), with all measurements being taken at a depth of 1 m.

The loch contains a resident population of small brown trout, Salmo trutta L. In previous years it had been stocked with rainbow trout and run as a put-and-take fishery for anglers, but there was no evidence that any of these rainbow trout were present in the loch prior to the present experiments. During these experiments all anglers fishing at the water were requested to complete a return form detailing the date and time of capture, number of fish caught (rainbow and brown trout), tag number of any tagged fish, method and location of capture, length, weight and any comments on the diet. An example of this return form is shown in Appendix D. These forms appeared to be more

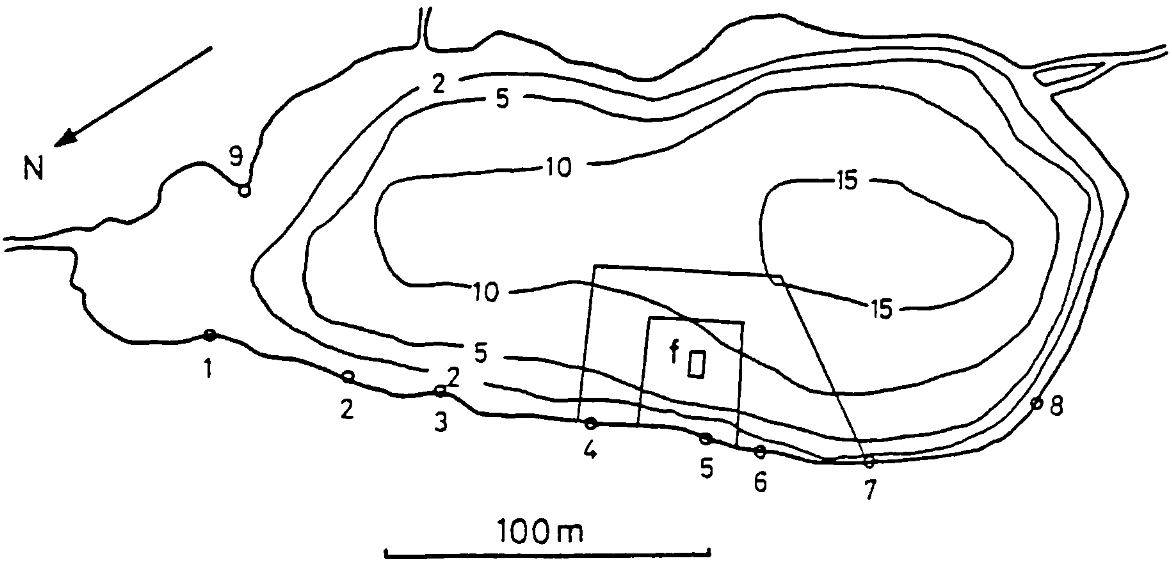


Figure 3.1. Loch Charn (Latitude 56°21'N, Longitude 5°31'W). Depth contours were obtained from plumb-line measurements at known positions. The areas around the feeding station (f) represent the areas where angling was prohibited up to 19 May 1980 (smaller area) and after this date (larger area). Circles and numbers on the bank denote stations from which most of the ultrasonic tag locations were taken.

Figure 3.2. Temperature in Loch Charn during 1980. Recorded at 1 m depth.

successfully completed when visits by the present author were more frequent. Thorpe (1974b) and Cane (1980) discuss some of the problems involved in using data from angling returns.

The feeding station consisted of an automatic feeder suspended from a raft constructed from scaffolding pipe and six buoys and was moored in 8.4 m of water 17 m directly out from the shore (Figure 3.1). In order to minimize angling close to the feeder an approximately rectangular (36 m x 32 m) floating rope cordon was moored around the feeding area. Anglers were forbidden to fish within this area. On 19 May 1980 it was extended to minimize further angling pressure on this area of the loch (Figure 3.1).

3.2.2. Experimental animals and pre-experimental procedure

Rainbow trout, Salmo gairdneri, which had been held in sea water at the facilities described in Section 2.2.1. were used for this series of experiments. Prior to being transferred to the loch, fish were starved for 2 days, anaesthetized in benzocaine (25 $mg.l^{-1}$ in sea water) and then individually weighed (nearest g), measured (fork length; nearest mm) and tagged. The tag consisted of an individually numbered plastic plate (4.5 mm wide x 15 mm long x 1 mm thick) attached to monofilament nylon. The tag was attached to the fish by threading the monofilament through the dorsal musculature approximately 5 mm below the base of the centre of the dorsal fin. The tagging technique is described in detail by Eisner and Ritter (1979) and some of the histopathological consequences by Roberts et al. (1973a,b,c) and Morgan and Roberts (1976). Yellow coloured tags were used in the first experiment and green coloured tags in the second. Prior to transfer to freshwater, fish were allowed at least 24 h to recover in the sea. Details of the stocks used are shown in Table 3.1.

Table 3.1. Details of the experimental fish stocked into Loch Charn.

No. of fish	Date of transfer	Date of release	Temp. of sea (°C)	Salinity of sea $^{0}/_{00}$	Temp of loch (°C)	Mean weight (g) (± ls.d)	Mean fork length (mm) (± ls.d)	Initial ration fed (% of b.w)
188	18 April 1980	23 April 1980	8.0	31	9.5	346 (± 131)	295 (± 38)	1.2%
172	8 Sept. 1980	12 Sept. 1980	14.0	25	16.0	235 (± 64)	261 (± 22)	1.85%

Rainbow trout were transported to the loch in oxygenated sea water and placed in a 2 m x 2 m x 2 m net suspended from the raft supporting the feeding station. Fish were then allowed between 4 and 5 days to recover from the stress associated with tagging and transportation and to acclimatize to fresh water. There was no mortality attributable to transportation and osmotic shock during these transfers.

Fish were released from the feeding station into the loch when they were feeding normally and consuming their calculated ration (Table 3.1) at one 15-min feed. Two top corners on one side of the net were released and the net gently tipped so that the fish could swim unharassed from the cage. The net was then checked for mortalities and removed from the feeding station.

3.2.3. Instrumentation

3.2.3.1. The feeding station

The underwater television camera described in Section 2.2.2. was attached to a Dexion frame and pointed vertically upwards. The frame was then suspended below the centre of the feeding station on four ropes attached to each of the corners of the feeding station raft. The water was more turbid in the loch than it had been in Dunstaffnage Bay and the camera would only give easily discernable fish silhouettes at a maximum depth of 2.5 m, giving a surface field of view on the video monitor of 17.7 m^2. The camera was connected via cable to the shore. The arrangement of the experimental apparatus is illustrated in Figures 3.3 and 3.4.

The feeder (Tess Aquaculture Ltd) consisted of a 100-l container at the bottom of which was a vibration plate driven by a 12 V motor. It was suspended approximately 0.5 m above the water surface on a scaffolding framework and was powered, via cable connections, by 12 V batteries on the shore.

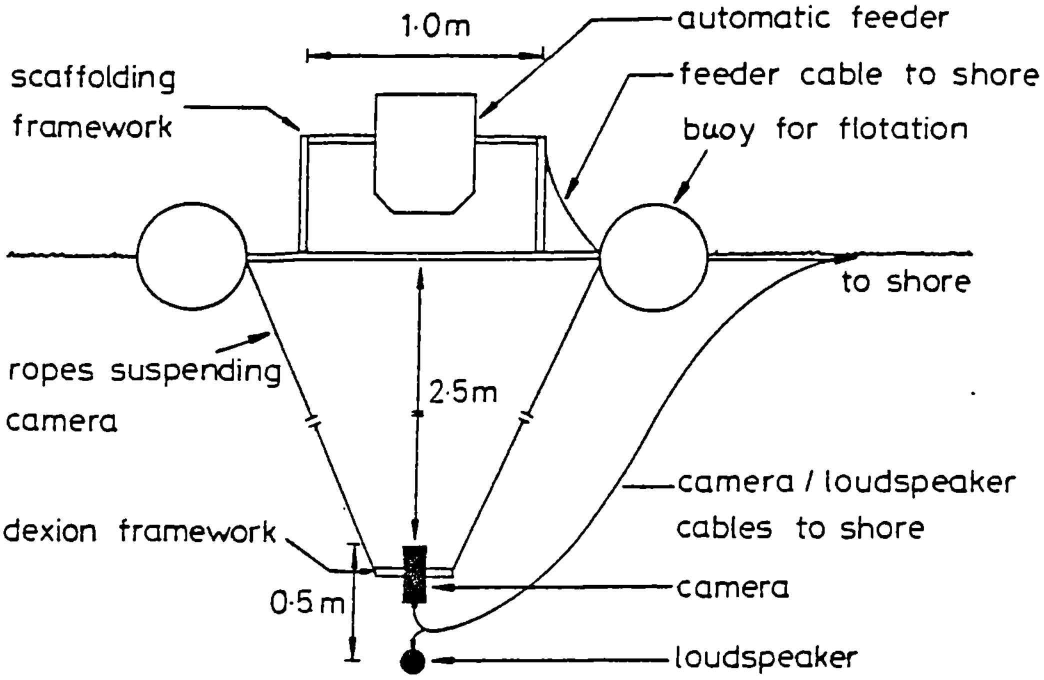


Figure 3.3. Diagram of the feeding station (the ropes suspending the loudspeaker are excluded). Six buoys provided flotation, only two of which are shown. The loudspeaker was absent during the experiments of Section 2.2.

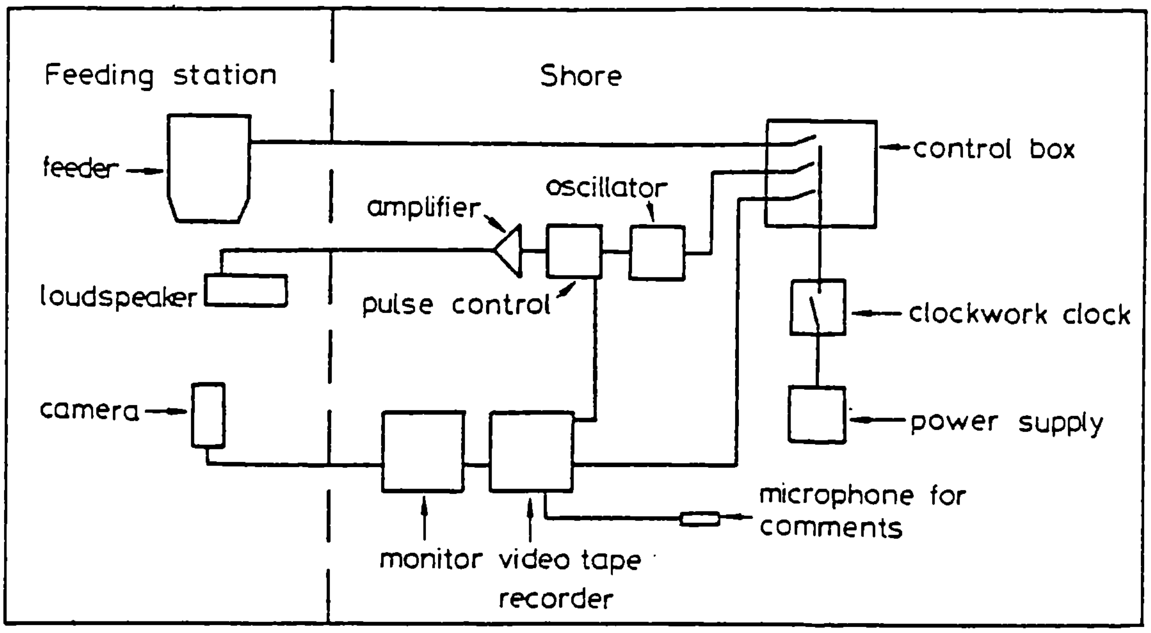


Figure 3.4. Block diagram of the apparatus used during the experiments in Loch Charn.

In the second series of experiments a J9 loudspeaker was suspended on two ropes from the scaffolding framework of the feeding station. It was held horizontally pointing in a north-north-easterly direction, mostly at 3 m, and connected via cable to the shore.

3.2.3.2. The shore

All equipment on the shore was contained in a large waterproof box. All of the equipment used was identical to that housed on the raft in Section 2, except that the power was supplied by two 12 V car batteries and the feeding sequence (video recording of fish behaviour prior to and during a feed, or prior to and during the conditioned stimulus and a feed) was initiated remotely by a programmable timer controlled by a clockwork clock (Appendix C).

Measurements of sound pressure and ambient noise were taken using the equipment described in Section 2.2.3.

3.2.4. Experimental Procedure

In the first experiment fish were fed at 0745, 0900, 1700 and 1815 BST (0800, 0900, 1700, 1800 up to 1/5/80) and in the second at 0845, 0930, 1600 and 1715 BST each day. Different times were taken in the latter experiments because the camera was not sensitive enough to record good pictures at the original times as a result of the decrease in daylength between the two periods. The timing of feeds was also varied within 1 h of these times during the ultrasonic tagging experiments.

There is evidence that rainbow trout are crepuscular in their feeding activity (Oswald, 1978) and prefer to feed at 7-or 8-hourly intervals (Adron *et al.*, 1973; Landless, 1974b, 1976a), so this morning and evening regime partly satisfied both requirements. The interval between the pairs of feeds was chosen as 1.25 h because early experiments suggested that this interval resulted in a good aggregation of fish in the field of view prior to the second feed.

Fish were fed floating trout food (Omega Trout Food; Floating Type; Edward Baker Ltd). The amount fed per day was calculated from the manufacturers tables (Appendix E) according to the total weight of fish stocked (Table 3.1). One quarter of this ration was fed at each feed. The amount was recalculated every 7 days taking into account temperature and the weight and growth of the fish removed from the loch. When none were recaptured by angling the growth of the fish in the loch was calculated assuming a food conversion ratio (amount of food fed ÷ weight gain) of 1.5 (Landless, 1979). This procedure estimated the weight of fish in the loch and allowed the required ration to be calculated. Where appropriate the actual ration level is stated in the text.

In the first experiment each feed consisted of one quarter of the daily ration being delivered at one time. In the second experiment the same ration was delivered but this was preceeded by a 1-min conditioned stimulus (details in later section). Prior to each food delivery the camera and video tape recorder were automatically and simultaneously switched on to record a sample of fish behaviour on video tape. Both were automatically switched off after a post feeding sample. More extensive video samples and comments concerning the video picture were recorded when the author was present. The number of rises (a fish breaking the surface to feed) to a food delivery in the feeding area was also counted during the early stages of the development of the response to the feeding station. Such observations were necessary in the first few days because fish were not always seen feeding within the camera's field of view.

3.2.5. Dietary analysis

Samples of the stomach contents of both rainbow trout and brown trout were recovered from fish captured by angling from 5 to 39 days after the first (23 April), and from 6 to 11 days after the second (12 September) stocking. All of these fish were captured by anglers outside the "forbidden" areas (Figure 3.1). After feeding was stopped on 6 August, 105 days after the April stocking, fish were captured by angling both inside and outside the feeding area. On this latter occasion and during September some fish were captured using artificial food as bait. After 6 August, even though there was no automatic feeding there was some hand feeding of fish in the feeding area during angling.

As soon as possible after capture all fish were measured (fork length; nearest mm) and usually weighed on a spring balance to the nearest 5 g. The oesophagus, stomach and intestine were then removed and placed in 70% alcohol. In the laboratory the contents of both the oesophagus and the stomach of individual fish were removed, pooled and preserved in 70% alcohol. Intestinal contents were also examined. The stomachs of 64 rainbow trout were examined.

Brown trout and their stomachs were also treated as above but in addition scales were collected from below the dorsal fin. These were later placed in water and examined under a low power microscope to determine the age of the fish.

All food items were identified to species where possible. The diet was then investigated using three methods of dietary analysis. First, a percent occurrence method was used in which the number of occurrences of a food item was expressed as a percentage of the total number of stomachs examined. Secondly, the number of items of a given type of food that were found in all specimens was expressed as a percentage of the total number of food items examined. Partially digested items were recorded as single organisms. This latter method is unable to take account of both trout pellets and plant material; the former often being found as an amorphous mass and the latter often being difficult to separate into individual components. For this reason this method was only used for the 'animal' components of the diet. A gravimetric method was also employed in which all items were dried to constant weight at 60^{o}C and the relative importance of the major components of the diet assessed in terms of dry weight. If the dry weights are considered alone, however, a single stomach from a large fish full of pellets may substantially increase the relative importance of this component to the population as a whole. In order to take account of this likely bias the fullness of the stomach was assessed using a points method (Hynes, 1950; 0 for an empty stomach, 10 for a full, distended stomach) and a proportion of these points was allocated to each component (artificial, plant, animal food) according to their relative abundance in terms of dry weight. This measure is subsequently referred to as the dry weight index. The relative merits and disadvantages of all of these methods (except the dry weight index) are discussed by Windell and Bowen (1978) and Hyslop (1980).

3.2.6. Growth rate

Fork lengths of fish were used to determine growth rates because this measurement is more accurately recorded and less prone to variation than wet weight which can show considerable differences as a result of variations in body water content and stomach fullness (Lagler, 1978).

Specific growth rate (s.g.r.) was calculated according to the following formula from Brown (1946) :

$$\text{s.g.r.} = \frac{(\log_e Lf - \log_e Li) \times 100}{T}$$

where Lf = final length (mm)

Li = inital length (mm)

T = time (days) since introduction into freshwater

Time was taken from the day the fish were placed in the net in freshwater because they were fed from this day.

3.2.7. Ultrasonic Tagging

3.2.7.1. Tags and receiving apparatus

Four fish were equipped with ultrasonic tags during the second experiment. Details of these fish are shown in Table 3.2. The pulsing Mark 3 ultrasonic tags described by Young *et al.* (1976) were used although they were shaped in the manner described by Ross *et al.* (1981). The first two fish (F1, S1; Table 3.2) were tagged with tags powered by two 45 mAH Mercury cells (Mallory RM 312). Because of premature tag failure as a result of battery malfunction and to prolong active life, one of these batteries was replaced by an 120 mAH cell (Mallory WH 8) on each of the other two tags. The frequency of the tags was in the range 240-260 KHz and the pulse repetition rate was varied (Young *et al.*, 1976) to produce individually recognisable tags. In this way two fish could be tracked at the same time, although this was difficult when two tagged fish were very close together.

The tag was attached to the fish immediately below the dorsal fin in the same way as the numbered tags described previously (Section 3.2.2.). The attachment technique is described by Ross *et al.* (1981). A plastic backplate was also attached on the opposite side of the tag which allowed the monofilament to be tied tightly and helped to minimize skin chafing.

Fish were tracked using the portable tracking system described by Young *et al.* (1976). Two hand held directional hydrophones were used and each had a built in amplifier that was connected to a receiver and loudspeaker. The position of a tagged fish was ascertained using the following techique. First, assume the hydrophone is correctly tuned and receiving a signal from a stationary fish. If the hydrophone is then rotated in the horizontal plane three maximum amplitude peaks are discernable. If the gain control of the loudspeaker amplifier is then carefully reduced only one (central) peak is evident and this represents the direction in which the fish lies. This direction

Table 3.2. Details of ultrasonically tagged rainbow trout.

Fish code	Time (BST) & date of tagging	Time (BST) & date of release	Fork length (mm)	Weight (g)	Observation terminated	Notes
F1	1600 10 Sept. 1980	1340 12 Sept. 1980	287	327	15 Sept. 1980	Released at feeding station with rest of stock of fish.
S1	1600 10 Sept. 1980	1340 12 Sept. 1980	287	333	15 Sept. 1980	"
F2	1800 22 Sept. 1980	1830 22 Sept. 1980	298	---	28 Sept. 1980	Captured & released at northern bay.
S2	1800 22 Sept. 1980	1830 22 Sept. 1980	274	---	11 Oct. 1980	Captured & released adjacent to feeding station

was quantified by taking its compass bearing and noting the position from which it was taken. Two observers with VHF radios were used simultaneously to record two bearings, so that the position of the fish could be 'fixed'. For maximum accuracy the observers moved their positions so that the fish lay at the apex of a right angled triangle; the observers forming the other two corners. All fixes were taken from known positions in the water next to the bank (Figure 3.1) and nearly all of these could be taken from the north-west shore.

The accuracy of the system was greatly reduced when fish were active because at these times it was difficult to obtain simultaneous fixes. It was also more difficult when there was a lot of background noise from wind and rain.

Details of the fixes were returned to the laboratory and plotted on a large scale map using standard triangulation techniques.

3.2.7.2. The experimental animals

Two large fish (F1 and S1) (Table 3.2) were selected from the net in the loch and tagged 2 days prior to the release of all the fish. Ultrasonically tagged fish are hyperactive for up to 48 h post-tagging (Young et al., 1972; Holliday et al., 1974; Hawkins et al., 1974; Priede and Young, 1977) so a two day settling down period should have overcome this problem and provided reliable data on the behaviour of recently stocked fish.

When the first two tags failed, two more fish (F2 and S2) were captured by angling and tagged. One was captured next to the feeder and one in the northern bay and both were released within 30 min of capture in the same positions to see if any fixed pattern of distribution had been reached at this time. Because of the 48-h post-tagging problem data from the first 2 days was ignored during the subsequent analysis.

3.3. RESULTS

3.3.1. The behaviour of rainbow trout with respect to a feeding station without a pre-feeding sound stimulus

3.3.1.1. Introduction

The aim of the work described in this section was to examine the relationship between stocked rainbow trout and a single supplementary feeding point. Particular attention was paid to the development of the response to the feeding station, the distribution of fish around the feeding station and the factors controlling this distribution.

3.3.1.2. Methods of analysis

Samples of fish behaviour were recorded automatically on video tape for 3 min both prior to and after feeding. Analysis of these tapes was difficult on clear days because the sun obscured part of the field of view and the resulting contrast between the sun and the remaining picture was too great. Samples were also occasionally missed as a result of battery failure although on only one occasion was the feeder also stopped.

Analysis consisted of counting the maximum number of fish within the field of view during the pre- and post-feed period by splitting the video tape into 10-s samples, counting the number at the beginning and end of each sample and, using slow video playback, noting the flux of fish into and out of the field of view during this time. Details of particular analytical techniques are given in each relevant section. In the following text, unless it is otherwise specified, day n (post-stocking) refers to the nth day after release of the fish into the loch.

Figure 3.5. The development of the response to the feeding station.

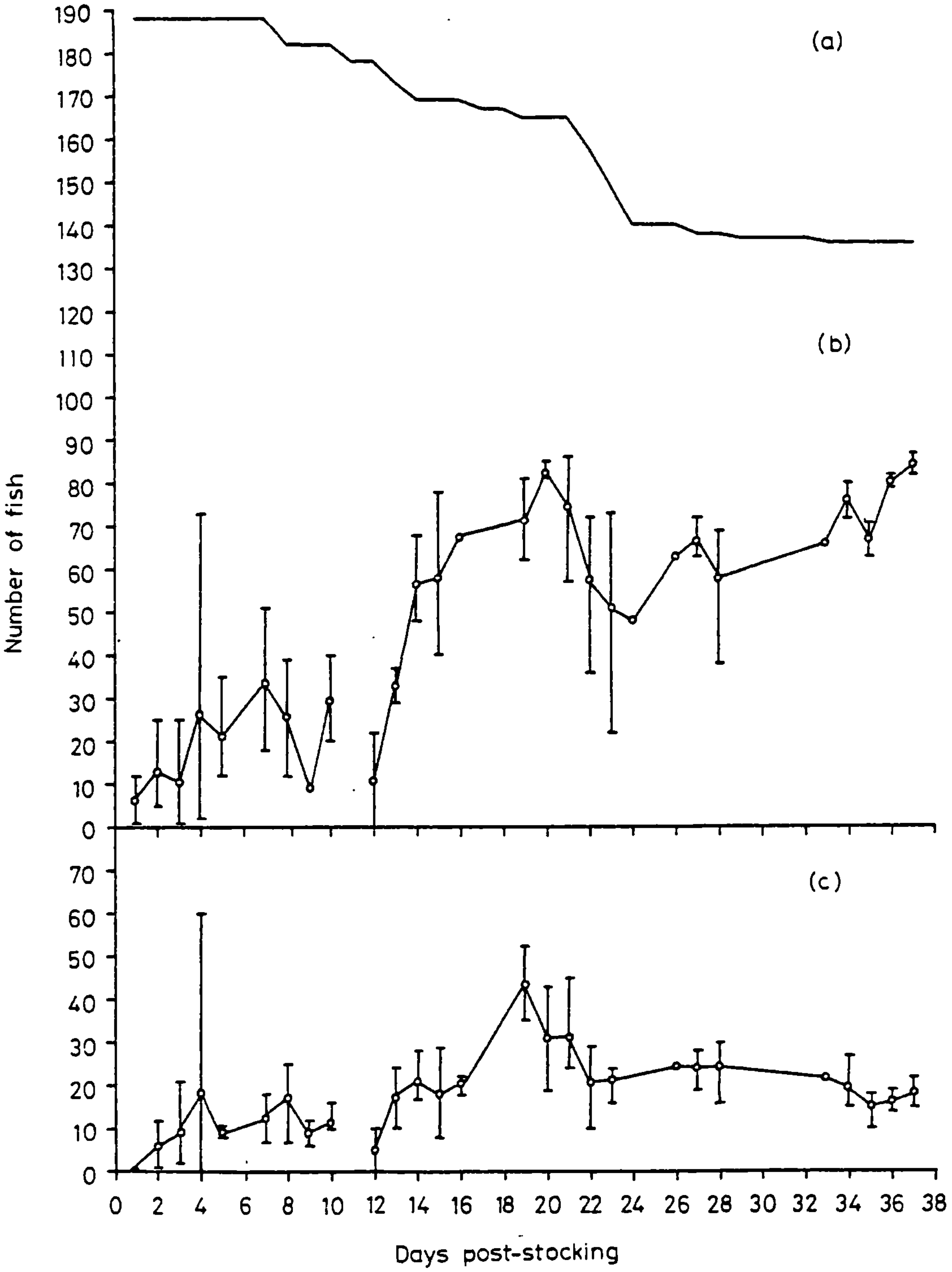
(a) shows the maximum number of fish in the loch estimated from the angling return forms (corrected on the day after any fish were captured).

(b) shows the mean and range of the maximum number of fish counted at the feeding station post-feeding.*

(c) shows the mean and range of the maximum number counted at the feeding station pre-feeding.*

No food or video samples on day 10 (1815), day 11 (all day) and day 12 (0745, 0900).

* The points without range bars represent single observations


(a)
(b)
(c)
Number of fish
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
Days post-stocking

3.3.1.3. The development of the response to the feeding station

There was an increase in the maximum number of fish counted in both the pre-and post-feeding period over the first 37 days, which reflected an increasing tendency to aggregate at the feeding station (Figure 3.5).

To learn to aggregate fish had to be attracted to the feeding area and this was initially accomplished by food drifting away from the feeder which stimulated activity over a wide area. For example, after the 1700 feed on day 1, fish were seen rising to artificial food, drifting in a slight current and blown by the wind, over a wide area both inside and outside of the feeding area. When food was spread away from the feeding station in this manner rises were usually aggregated into bouts of feeding activity. This behaviour was a result of both an uneven distribution of food within the feeding area and the behaviour of the rainbow trout, because video observations showed that an individual rising to food simulated feeding activity within a particular area by drawing attention to the area and/or exciting other fish to feed in the area. Fish often entered the camera's field of view in small groups and if they were feeding in such groups this would also have given rise to more distinct bouts of activity.

There was an increase in the number of rises within the feeding area in the first 6 min after food was delivered at 1700 on day 2. This increase was a result of food spreading out from the feeder and fish being attracted to the feeding area (Figure 3.6). After feeding over a wider area these fish then aggregated much closer to the feeding station and there was an increase in the number of fish counted on the video. (On the basis of this result, 1.25 h was chosen as the interval between feeds from day 8 onwards). Continual reinforcement of the attraction to the food source would tend to improve the aggregation and on subsequent days the response became much more localized (Figure 3.7).

Figure 3.6. Observations of the response to a food delivery at 1700 on day 2.

(a) shows the total number of rises within the feeding area. The rises, which consisted of a splash on the surface, were counted by eye and were totalled for each 2-min period.

(b) shows the maximum number of fish seen on the video screen per 2-min period and represents the number of fish seen in the immediate vicinity of the feeding station.

No observations from 34-40 min post-feeding.

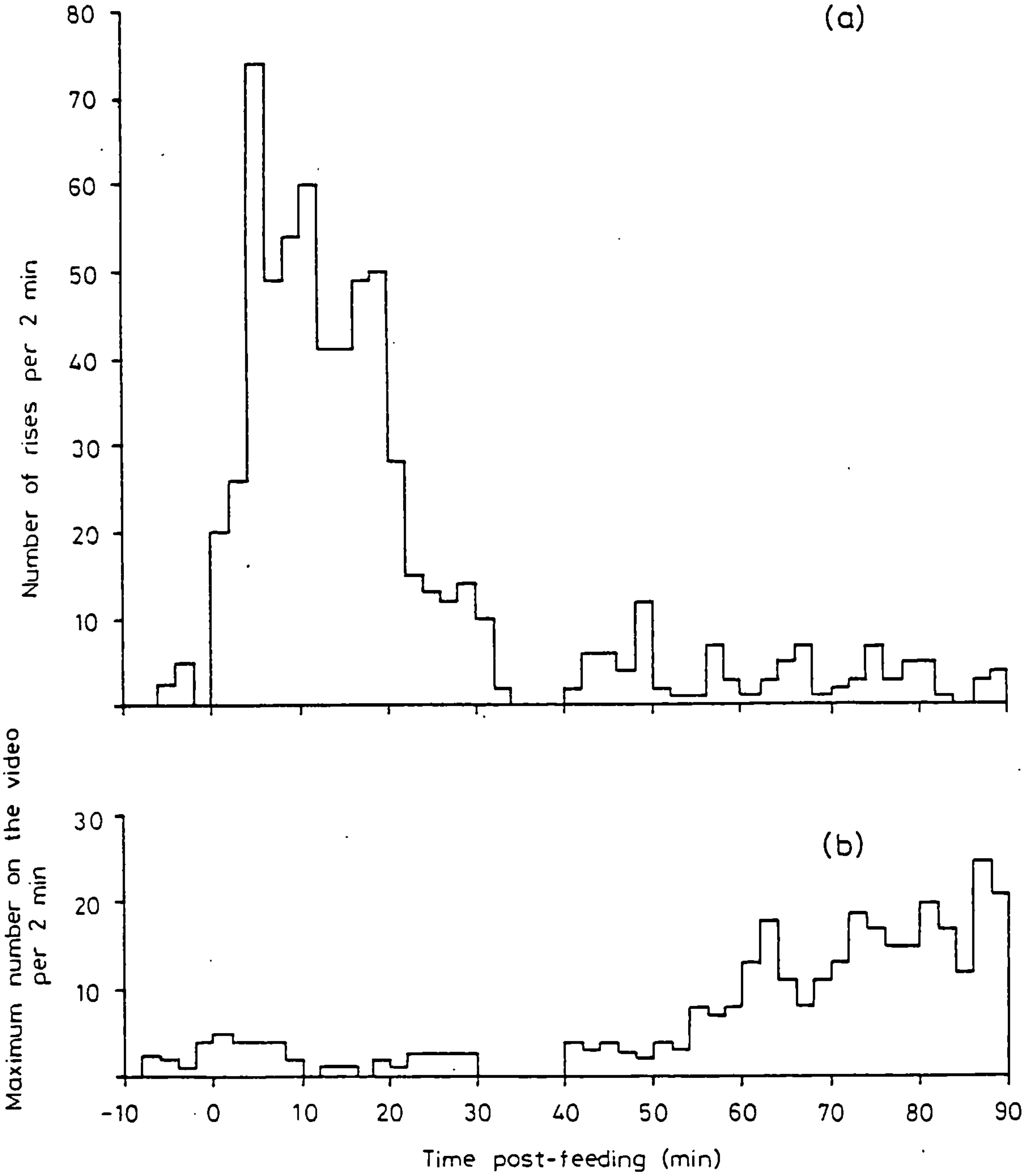
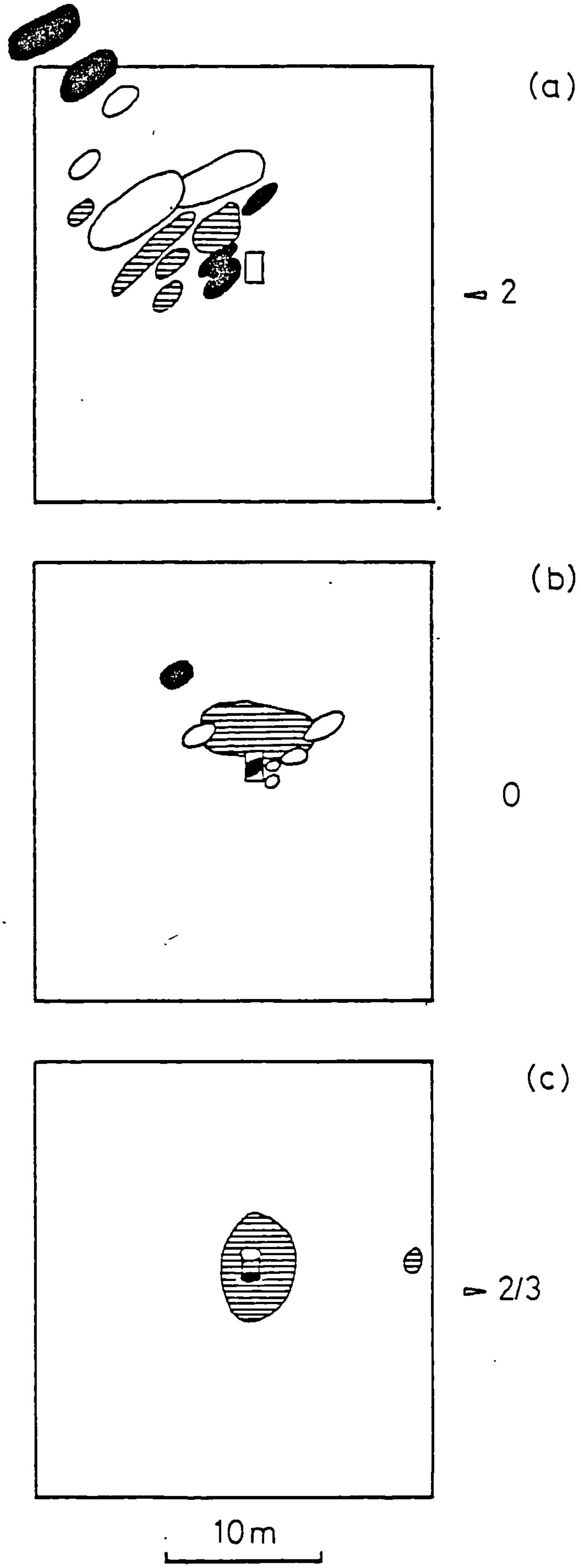

(a)
Number of rises per 2 min
80
70
60
50
40
30
20
10
(b)
Maximum number on the video per 2 min
30
20
10
-10
0
10
20
30
40
50
60
70
80
90
Time post-feeding (min)

Figure 3.7. The approximate position of feeding bouts during the early development of the response to the feeding station. The observations were made at 1700 on day 2(a), day 3(b) and day 5(c). Arrows denote the approximate wind direction and Beaufort scale force. The outlined areas show the areas in which feeding activity was observed after a food delivery at the feeding station.

Observations, which were made for 30 min on each occasion, were divided into 0-10 min (▤), 10-20 min (□) and 20-30 min (■) periods after the food delivery. For clarity, the areas inside the feeding station in (c) are separated although in reality they were superimposed on one another.


(a)
2
(b)
0
(c)
2/3
10m

As no fish were seen rising to hand thrown pellets in the loch before the rainbow trout were released all the rising fish, initially at least, probably derived from this stock. This view was confirmed when tagged rainbow trout were seen at the feeding station on several occasions whilst the feeder was being serviced.

The increased localization of the response, nearer to the feeding station, was, apart from the continual reinforcement, also due to the fish becoming increasingly familiar with the apparatus. Before day 5, the fish were often seen moving quickly into the camera's field of view to feed before rapidly moving out again. This behaviour was rarely observed after day 5 when fish readily fed within the centre of the field of view.

There was a decrease in the time taken to reach the maximum number of rises per 30 s and an increase in the maximum number of rises at this peak during the first 5 days (Figure 3.8) showing that more fish were remaining closer to the feeding station during this period. In addition, fish may also have learnt that feeding activity signalled that food was available at the feeder and consequently responded to any such activity by moving to the feeding station.

After the short period of starvation the time taken to reach the maximum number of rises increased to 2.5 min (see arrow in Figure 3.8) suggesting that the fish had moved away from the feeding station during this period and that food was required to maintain this aggregation.

The increase in the number of fish feeding at the feeding station was not solely due to fish aggregating and remaining close to the feeder. During the early development of the response some fish spread away from the feeder after feeding. For example, on day 4, 73 fish were attracted into the field of view at the 0900 feed although on the next feed (1700) a maximum of only two were seen in the 3-min post-feeding video sample. The occurrence of fish with pellets in their stomachs throughout the loch (Section 3.6.2. ; Figure 3.28) confirmed this movement.

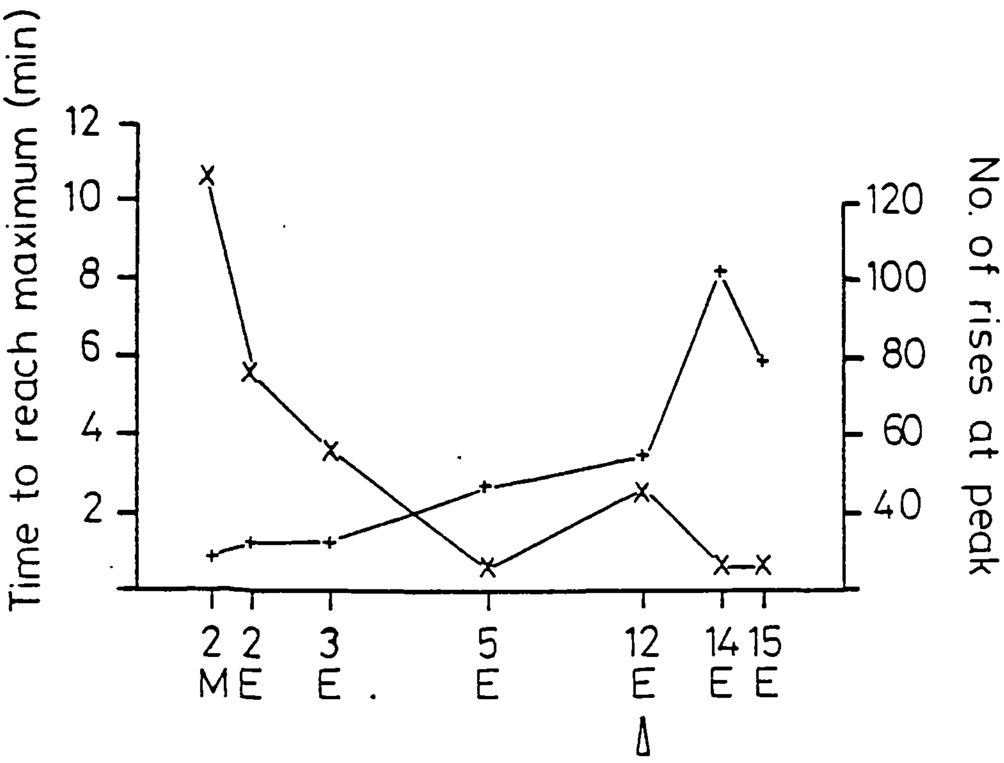


Figure 3.8. The change in the pattern of rises within the feeding area. The graph shows the time taken to reach maximum (peak) numbers of rises per 30 s period (LH axis), and the number of rises at this peak (RH axis). The abscissa shows the day post-stocking and whether the observations were made on the first of a morning (M) or evening (E) pair of feeds. The arrow indicates the first feed after 7 feeds starvation.

The tendency for fish to drift away from the feeding station after feeding affected the variation in the maximum number of fish that were counted in the individual feeds making up each pair of feeds (Figure 3.9). The large scatter of points between days 0 and 10 in this figure is partly due to the smaller numbers involved but is also due to a large number of fish being attracted into the feeding area after the first feed and being recorded on the second of each pair of feeds. After this time there was less of a difference between the numbers attracted on the two feeds suggesting there was a more consistently sized group at the feeding station.

A variable plateau in the maximum number of fish seen after a food delivery was reached after approximately 14 days. This plateau may have been reached one or two days earlier if there had not been a battery failure, and hence no food deliveries, from 1815 on day 10 until 1700 on day 12. The variation in the level of this plateau was partly due to a variation in the numbers feeding, in their aggregation during feeding and sampling errors inherent in the analysis of poor quality video recordings. The effect of a reduction in the apparent number of fish in the loch, as judged by the return of angling forms (Figure 3.5a), was not translated into any long term decline in the number feeding at the feeding station (Figure, 3.5b), although there may have been some short term effect (Figure 3.5b, days 21-24).

The increasing tendency to aggregate at the feeding station meant that the maximum number of fish counted on the video after a food delivery was seen much closer to the actual time of feeding. From day 19 onwards, the maximum number was always counted within 20 s of feeding and after this date there was a distinct aggregation at the feeding station (see following Section 3.3.1.4). This behaviour made it much easier to count fish as they entered the camera's field of view to feed and therefore, to conserve video tape, the video sample was reduced to a 1.5-min pre- and post-feeding sample from day 19

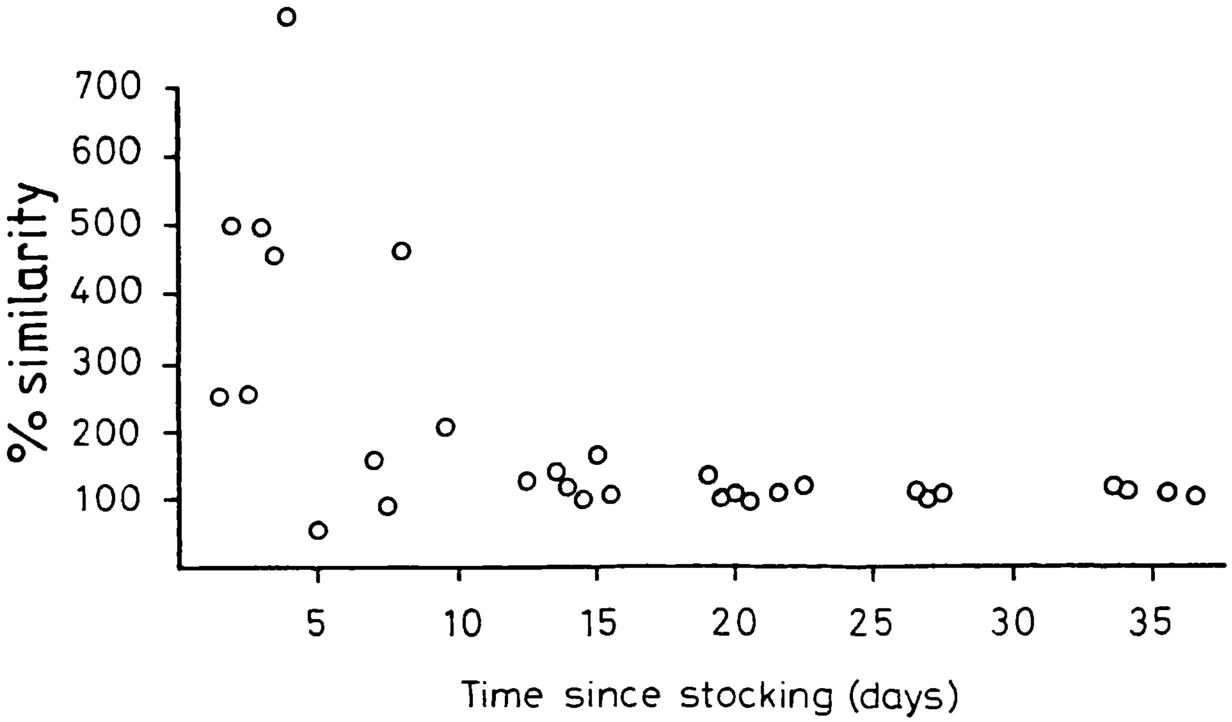


Figure 3.9. The change in the numbers seen in the television camera's field of view between each pair of feeds during the development of the response to the feeding station. Each point represents the maximum number seen feeding on the second of each pair of feeds expressed as a percentage of the maximum seen on the first feed.

onwards. As after day 5 the food was usually (and always after day 19) consumed within 1.5 min (mode 1.5; range 1.0-2.5 min; n = 10; day 5 - day 30), with the maximum number of rises on all normally timed feeds occurring within 30 s of feeding, this sample covered the major period of feeding activity.

The maximum number of fish recorded within the field of view on any one feed was 87, on day 37, and this accounted for 64% of the total number of fish in the loch at this time (136). In a later experiment, between days 99 and 103 (Section 3.5.2.), the camera was placed in a horizontal position just below the feeding station and a maximum of three brown trout were observed along with an abundance of rainbow trout tagged with yellow tags. Thus, rainbow trout constituted the overwhelming majority of fish at the feeding station and the decreasing angler catch rate (Figure 3.5a; Section 3.6.2; Figure 3.28) and increasing aggregation (Figure 3.5b,c) shows that, after stocking, the uncaught fish learnt to aggregate and remain close to the feeding station.

3.3.1.4. The distribution of fish around the feeding station

3.3.1.4.1. Introduction and methods

The aim of this section was to describe the spatial distribution of fish around the feeding station using data obtained from the video recordings at feeding times after and including day 19.

To investigate the distribution of fish around the feeding station the number entering the camera's field of view was counted at 1-s intervals immediately post-feeding. For each feed a cumulative total of the number entering was kept over the first 10 s and this number was expressed as a percentage of the maximum number counted up to 1.5 min post-feeding which, as mentioned earlier, was counted within 20 s of feeding after day 19. These data were then plotted as a cumulative percentage curve (Figure 3.10).

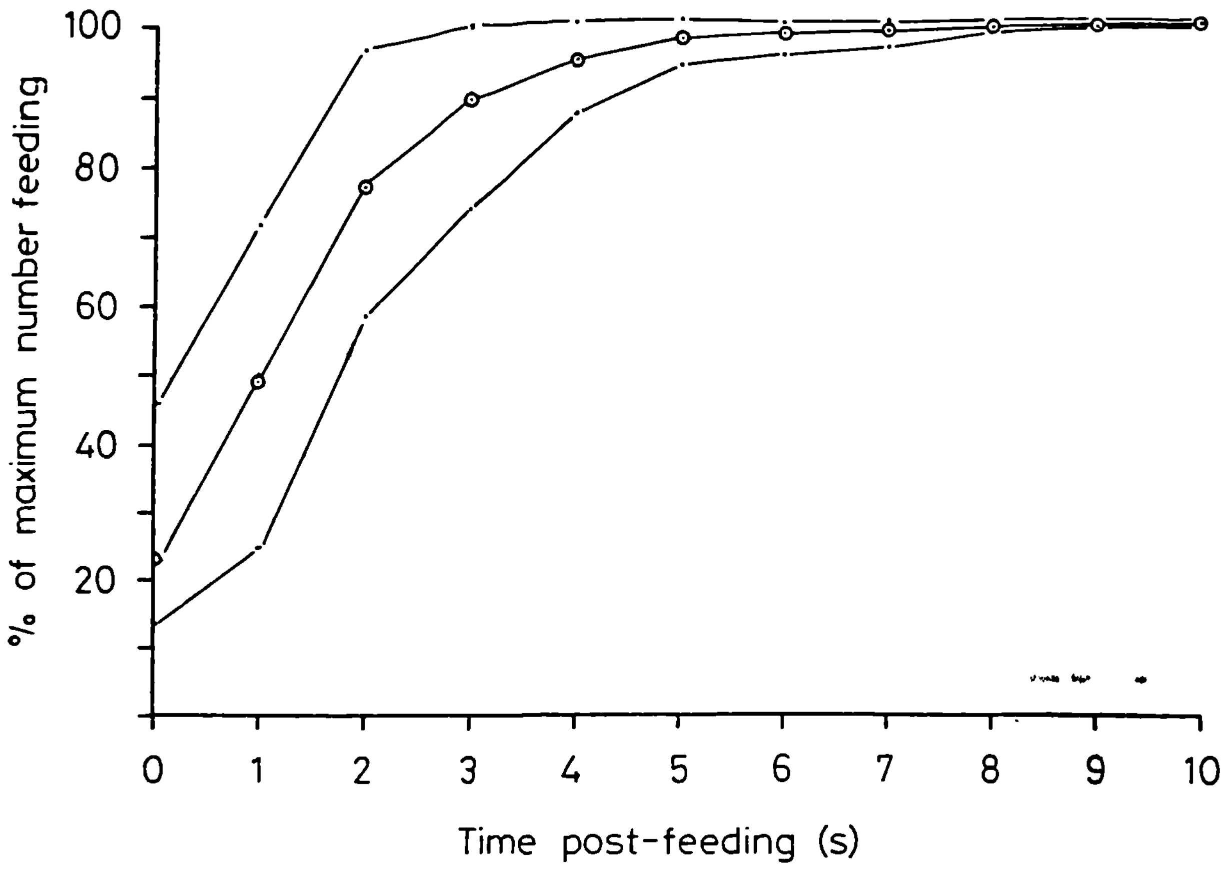


Figure 3.10. The distribution of fish around the feeding station as judged by the time at which fish entered the television camera's field of view. The graph shows the percentage of the maximum number counted on each feed that were observed within the field of view up to 10 s after a food delivery. The data derive from 13,1st feeds and 7,1st feeds observed between day 19 and 37 and day 95 and 99 post-stocking respectively.

ʘ represents the mean.

. represents the range.

A further analysis was carried out to determine whether there were any significant changes in the distribution of fish around the feeding station which were reflected in the cumulative percentage curve (Figure 3.10). This analysis fitted a binomial model to the entry times on each individual feed according to the equation :

$$\text{logit}\ \Theta = \log_e \frac{\Theta}{(1-\Theta)} = \alpha + \beta \log_e t$$

where Θ = the proportion of the maximum number of fish within the field of view at time t (the maximum number in this model was, for simplicity, taken as the maximum that were counted within 10 s of feeding).

α = an estimate of the intercept of a plot of $\log_e (\Theta/(1-\Theta))$ versus $\log_e t$.

β = estimate of the slope of the above line

t = time (s)

Since the model predicts that the proportion at $t = 0$ is zero then, before it was fitted, the number of fish present at $t = 0$ was subtracted from subsequent observations.

Four sets of data were used in this analysis (Table 3.3) and for each an estimate of the common slope was calculated using a computer programmed to carry out full maximum likelihood iterations (Hewlett and Plackett, 1979). The deviance (or sum of squares of the standardized residuals, Hewlett and Plackett, 1979) was then used to test the goodness of fit of the observed to the expected proportions. The significance of this value was assessed by reference to a table of χ^2 with (kn-n-1) degrees of freedom where k is the number of observations in each feed (10 in all cases) and n is the number of feeds in each data set. Analysis of covariance was used to compare the differences between the slopes of the various data sets (Snedecor and Cochran, 1978).

3.3.1.4.2. Results

If a group of fish of uniform density were distributed around the feeder and reacted to the feeding stimulus simultaneously, a linear model should

Table 3.3. The slopes associated with the binomial model describing the times at which a proportion of the maximum number seen feeding after 10 s entered the field of view. The data derive from three separate post-stocking periods and two different feeding times. There is no significant difference between any of these slopes (F = 1.043; d.f. = 3, 42; $p > 0.05$). For further details see Section 3.3.1.4.1.

(* = 10% rations, see Section 3.3.1.9)

All deviances, $p > 0.05$

Time of sample (days post-stocking)	1st or 2nd of each pair of feeds	n	Estimate of slope	Standard error of slope	Deviance
19-37	1	13	2.748	0.080	130.4
19-37	2	13	2.666	0.091	97.39
37-46*	1	13	2.965	0.119	85.58
95-99	1	7	2.831	0.134	59.12

describe the relationship between time and the percentage entering the field of view. In practice, this model is clearly limited both by the availability of fish and their ability to be absorbed into the centre of the field of view. However, the linear model appears to fit reasonably well for 2 s after feeding, but deviates markedly after this period (Figure 3.10). This change is attributable to both a decrease in the density of fish as one moves away from the immediate vicinity of the feeder and to an increased reaction time for fish further from the feeder. Because it fits well for the first 2 s after feeding and accounts for a mean of approximately 75-80% of those feeding it suggests that, on average, this percentage of feeding fish were distributed around the feeding station at a relatively constant density and that the remaining 20-25% were at a lower density and merged with the periphery of this group.

This distribution of the group at the feeding station remained relatively constant up to at least day 99 as there was no significant difference betwen the pattern of entry times between days 19 - 37 and 95 - 99 (Table 3.3). Data from this latter time were therefore incorporated into Figure 3.10.

Because of the flux of fish in and out of the field of view after 10 s, it was usually impossible to tell whether any outlying fish were joining the feeding group. To investigate whether there were any fish attracted to the area after the first 10 s the Wilcoxon test (Siegel, 1956) was used to test the null hypothesis that there was no significant difference between the maximum number of fish seen on the 1st and 2nd of each pair of feeds. The data used in this analysis were taken from clear feeds observed from day 19 onwards. There was a significant ($T = 29$; $N = 16$; $p < 0.05$) increase in the numbers counted on the second of each pair of feeds showing that the null hypothesis may be rejected and suggesting that there were several outlying fish that were not counted on the first of each pair of feeds (mean number attracted = 2.7; range = -6 to +19). This difference was not a short term phenomenon related to the development of the response to the feeding station as four pairs of feeds were observed from day 95 to day 99 and on all of these occasions less fish were seen on the first than on the second of each pair of feeds (mean number attracted = 4.0; range = 2 to 6) (these data were incorporated into the above analysis). As there were no angling returns during this period, however, these fish probably did not stray outside of the "forbidden" area around the feeding station.

The camera was removed on 13 June (day 51) and no video observations were made until 27 July (day 95), when a series of feeds were recorded to check the long term stability of the feeding group. A maximum number of 44 fish were recorded (mean = 39.2; range = 29-44; n = 13) which represented 33.9% of the apparent number of fish in the loch as judged by the angling return forms. Up to three of these fish may have been brown trout (Section 3.6.7.2.). This percentage is undoubtedly an error, because after these video samples were taken, 43 rainbow trout of this stock were removed by angling, mostly around the feeder, suggesting that the fish aggregating around the feeder station (44 -3 brown trout) represented at least 95.35% of the rainbow trout in the loch. The large discrepancy between these two percentages must be due to incomplete reporting of angling returns and perhaps some natural mortality, although the result again illustrates the fact that the decrease in angling returns was due to an aggregation of fish around the feeding station rather than a total reduction in the available fish.

3.3.1.5. The circular distribution of fish around the feeding station

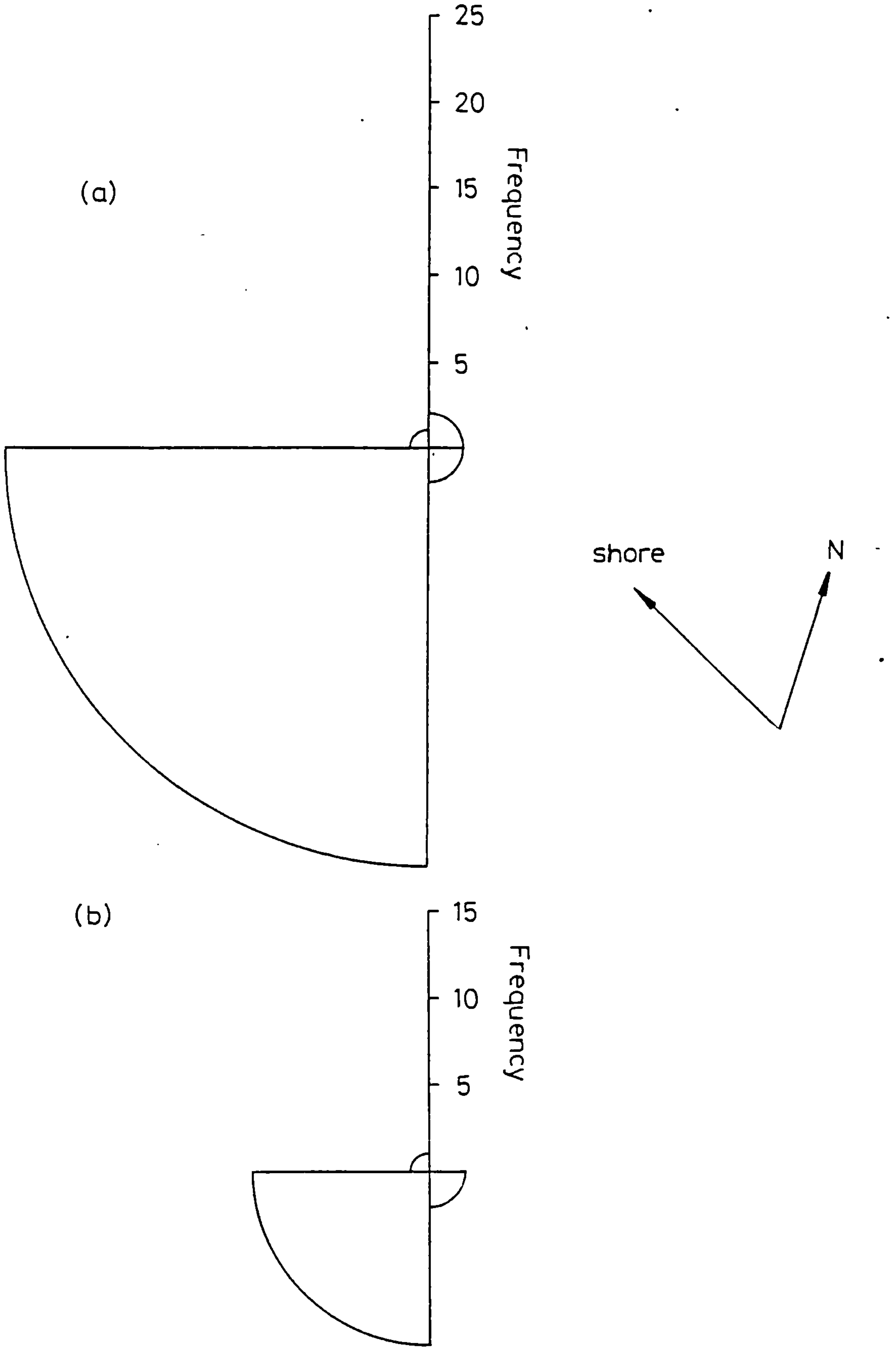
3.3.1.5.1. Introduction and methods

The aim of the analyses performed in this section was to determine if the fish were uniformly distributed around the feeding station. To do this the video monitor screen was divided into four equal sectors and the number of fish that entered each sector was counted on each feed. Ranks were then assigned to

Table 3.4. The total of the ranks and Kendall's coefficient of concordance (W) for the number of fish entering the four sectors to feed at the feeding station.

Time of sample (days post-stocking)	Sector 1	2	3	4	n	W	p
days 19-37	72	92	37	89	29	0.526	< 0.01
days 95-99	46	35	16.5	32.5	13	0.555	< 0.01
both combined (days 19-99)	118	127	53.5	121.5	42	0.265	< 0.01

Figure 3.11. The distribution of fish around the feeding station between days 19 and 37(a) and days 95 and 99 (b). The sector into which the greatest number of fish entered was recorded at each feeding time and the diagrams show the number of times each sector contained this maximum number. The data derive from 29 (a) and 13 (b) feeds.


(a)
25
20
15
10
5
Frequency
shore
N
(b)
15
10
5
Frequency

each sector on every feed according to the relative number of fish entering each of them (1 for most fish to 4 for least fish). The similarity of the rankings within and between two data sets (data set 1; days 19-37; data set 2; days 95 - 99) was then compared using Kendall's coefficient of concordance (Siegel, 1956).

3.3.1.5.2. Results

Within and between both data sets there was a significant similarity in the rankings with a consistently greater number of fish entering Sector 3 (Table 3.4). This result suggests that Sector 3, which is on the south-western side of the feeder (Figure 3.11), was a consistently preferred area from day 19 to day 99 and the group of fish were not uniformly distributed around the feeding station.

3.3.1.6. The area covered by the group at the feeding station

3.3.1.6.1. Introduction and methods

From the distribution of times taken to enter the field of view at feeding times (Figure 3.10), it appears that fish close to the feeder formed a distinct group with a few outlying individuals. An approximation of the area covered by this group and the distance at which they were found from the feeding station can be made using the following methods.

Method 1

Assume that the mean density of fish in the field of view before each trial is equal to the mean density of fish outside the field of view. The area covered by the group (X) may then be estimated using the formula:-

$$X = \bar{d} \times F_{max}$$

where $\bar{d}$ = mean pre-trial density (m^{-2})

F_{max} = maximum post-feeding number.

Method 2

The velocity of, and the time at which fish enter the field of view, may be used to calculate the distance from which they have travelled according to the formula:

$$D = D_A + V \times (T - T_F - T_R)$$

where D = distance travelled (m)

D_A = distance travelled to reach constant velocity (m)

V = velocity ($m.s^{-1}$)

T = time taken to enter field of view (s)

T_F = time taken to reach constant velocity from stop (s)

T_R = time taken to start to react after food is introduced (s)

Because the exact three-dimensional position of the fish was unknown, velocity could not be measured directly. If the size of the fish is known, however, velocity can be estimated indirectly from the tail beat frequency, providing this is greater than 2.5. s^{-1} (Webb, 1971). The formula, given by Bainbridge (1958), is:

$$V = \frac{1}{4} L (3f-4)$$

where V = velocity ($m.s^{-1}$)

f = tail beat frequency (s^{-1})

L = body length (m)

Body length was taken as 0.30 m (fish were stocked at a mean fork length of 0.295 m; the data considered here is from fish observed from day 19 onwards) and Da and T_F may be approximated from Webb (1976) who gives values of 0.1 m and 0.1 s respectively for a 0.3-m rainbow trout. T and T_R was measured from the video tapes although the reaction time of fish in the field of view would have been less than that of those outside the field of view.

3.3.1.6.2. Results

Method 1

To calculate the mean pre-feeding density the video tape was stopped at 10-s intervals over a 1.5-min pre-feed sampling period. The mean of this value was then divided by the surface field of view of the camera (17.7 m^2) to give a mean density. All the data used were from day 19 onwards.

From day 19 until day 37 the mean area covered on the first in each pair of feeds was 89.00 m^2 (s.d. = 29.34 m^2; n = 15). There was no significant correlation between the size of this catchment area and time over this period (tau = 0.314; n = 15; $p > 0.10$). From day 95 until day 99 the mean area was 105.19 m^2 (s.d. = 15.73 m^2; n = 7). There was no significant difference between these two means (t = 1.359; d.f. = 20; $p > 0.1$) suggesting that there was no significant change in the size of area occupied between these two periods which agrees with the results of Section 3.3.1.4. There was, however, a significant difference between the mean pre-trial density on the first of each pair of feeds during the two sampling periods (day 19 - day 37; $\bar{d} = 0.83$ m^2; s.d. = 0.23 m^2; n = 15) (day 95 - day 99; $\bar{d} = 0.395$ m^{-2}; s.d. = 0.07 m^{-2}; n = 7) (t = 4.843; d.f. = 20; $p < 0.001$). This result suggests that the area covered by the feeding station group may have been relatively constant and independent of the numbers of fish present or it may have been coincidental with the larger fish, after 95 days, requiring a greater individual 'living space'.

The area covered immediately prior to feeding was less on the second of each pair of feeds. The significance of this within pairs trend was tested using the Wilcoxon test. The observed distribution was tested against the null hypothesis that there was no significant diference between individual feeds within a set of pairs of feeds. Data from day 19-day 37 and day 95-day 99 were combined and used in this analysis. The result (T = 12; N = 16; $p < 0.01$) (mean difference = 15.55 m^2; range -14.19 to 35.93) shows that the null hypothesis may be rejected suggesting a contraction of the area covered prior to the second feed in each pair. This result does not agree with the results of the binomial analysis of entry times (Table 3.3) but this difference is probably a reflection of the greater sensitivity of the present analysis which is able to take account of differences between individual pairs of feeds rather 1st and 2nd feeds as a whole.

Method 2

The mean reaction speed of fish within the field of view was 0.178 s (s.d. = 0.078; n = 30). The mean tail beat frequency (average of 5 tail beats for 20 fish) was $10.67.s^{-1}$ (s.d. = $2.0.s^{-1}$; n = 20). The mean velocity, from Bainbridge (1958), is therefore 2.10 $m.s^{-1}$. The distance travelled (D,m) after a given time (T, s) can therefore be estimated with the formula:-

$D = 0.10 + 2.10 (T - 0.10 - 0.178)$.

On average between 75 and 80% of the fish entered the field of view within 2 s and approximately 95% within 4 s (Figure 3.10). These fish would therefore have travelled a distance of 3.7 and 7.9 m respectively. These estimates will be maximum distances because fish further away would have reacted slower than those in the field of view and because of the rectangular field of view of the camera there will be a maximum error on these distances of 1.15 m (the difference between the distance to the centre of the field of view from the nearest side to the farthermost corner of the video monitor screen). As the maximum distance from the feeder to the edge of the field of view was 2.55 m this analysis suggests that approximately 95% of the group at the feeding station lay within 10.45 m of the feeder. This figure corresponds to a circular area of 343.2 m^2 covered by 95% of the group at the feeding station.

Comparison of methods 1 and 2

Both methods incorrectly assume a two dimensional picture. In the first method the density per unit area will be greater (therefore the real value of the area covered is less) because of the limited conical field of view of the camera but this limitation will, to some extent, be offset and perhaps over-balanced by the non-uniform distribution around the feeding station because density is less at the edges (Section 3.3.1.4.). The area calculated using method 2 is greater than that calculated using the first method. The difference is both due to an increased reaction time for fish farther from the feeder and the fish being non-uniformly distributed around the feeding station with the latter probably being the most important factor. Therefore, the first method probably gives a better approximation to the area covered although the second method gives a useful approximation of the maximum distance over which fish were travelling to feed.

3.3.1.7. The distribution of fish around the feeding station between normal feeding times

3.3.1.7.1. Introduction and methods

Previous sections have discussed the behaviour of fish around the feeding station at feeding time. This section describes the distribution around the feeder at other times. The information is restricted to daylight hours because the camera is insensitive to low night-time light levels.

To examine the distribution outwith normal feeding times food was introduced from the feeder at unusual feeding times. Apart from the time of feeding other details remained as normal with a 1.5 min pre- and post- feeding video sample. The maximum number feeding at the unusual feeding time was then compared with the mean of the maximum number of fish counted at the four normal feeding times on either side of it using the Wilcoxon test.

3.3.1.7.2. Results

The maximum number at the unusual feeding time was always less than those counted during the four feeds on either side of this time (Table 3.5). The

Table 3.5. A comparison of the maximum number feeding at unusual feeding times with the maximum number counted on the feeds either side of these times. (* = 10% rations, see Section 3.3.1.9.)

Day and time of unusual feed (BST)		Number at unusual feeding time	Mean number counted feeding at the normal feeds either side (n = 4) (range in brackets)
27	1245	52	65.5 (63 - 72)
16	1300	61	67.5 (67 - 68; n = 2; 0745/0900 feeds)
24	0600	7	35.0 (22 -48; n = 2; 1815/0745 feeds)
41	2100*	14	39.5 (37 - 44)
42	1215*	26	37.5 (31 - 44)
97	0600	9	36.75 (29 -42)

difference between the maximum unusual feed number and the mean of the feeds either side is significant (T = 0; N = 6; p = 0.05) suggesting that fish were moving away from the feeding area between normal feeding times or were satiated and less responsive at these times.

Because of the small sample conclusions based on these data are tentative. There was, however, no evidence of a significant change in the entry times or size of the area covered by the feeding group during the midday period suggesting that the aggregation at the feeding station remains relatively consistent during the day. The greatest difference in numbers was observed when the unusual feeding time was after the evening and before the morning feeds which strongly suggests that the fish were further away at these times or, at the lower light levels, they were not attracted to the feeder as efficiently as they were during normal daylight hours.

3.3.1.8. Diel patterns in the movement of fish at the feeding station

3.3.1.8.1. Introduction and methods

The results of the previous section suggest that if the numbers of fish were reduced at unusual feeding times but regained prior to normal feeding times there must have been some entrained rhythm of movement around the feeding station.

The aim of the experiments described in this section was to investigate whether there was any such rhythm by recording 24-h changes in the number of fish within the camera's field of view.

Video samples of fish behaviour of 1.5 to 3 min duration were automatically recorded every 1.25 h during daylight hours. In each sample the number of fish within the field of view was counted at 10-s intervals and a mean and standard deviation was calculated for each sample.

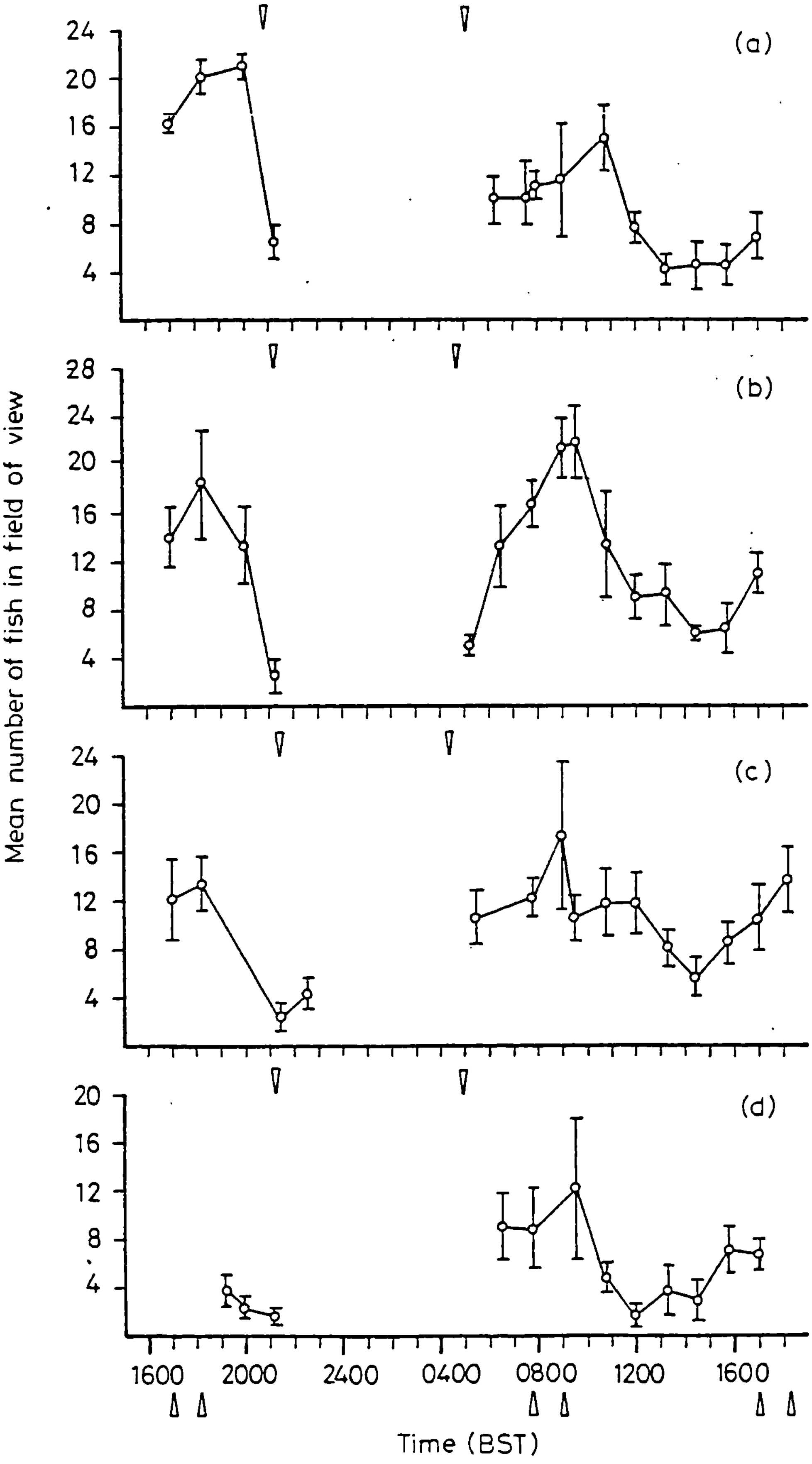
Figure 3.12. Diel variations in the number of fish seen at the feeding station. Downward pointing arrows indicate sunset and sunrise times. Upwards pointing arrows show feeding times. Each point represents the mean (± 1 s.d.) of counts taken every 10 s during the sampling periods that are indicated below.

(a) day 14 - 15 ; 1.5 min samples.

(b) day 26 - 27 ; 1.5 min samples.

(c) day 40 - 41 (10% ration level) ; 3.0 min samples.

(d) day 98 - 99 ; 2.5 min samples.


(a)
(b)
(c)
(d)
24
20
16
12
8
4
28
24
20
16
12
8
4
24
20
16
12
8
4
20
16
12
8
4
Mean number of fish in field of view
1600
2000
2400
0400
0800
1200
1600
Time (BST)

3.3.1.8.2. Results

The results (Figure 3.12) suggest a rhythm associated with the feeding times with a clear decrease in density after feeding time and a less obvious increase in the density of fish close to the feeder before, and perhaps in anticipation of, feeding time. The lowest densities were recorded late in the evening which agrees with the results of the previous section. No manipulation of feeding times was attempted to enable the peaks to be correlated with feeding time but the results strongly suggest that this is the case.

Spreading out after feeding was probably accomplished through aggressive interactions and passive dispersal. On occasions an aggressive individual was observed directly below the feeder and this fish may have increased the rate of dispersal in a similar way to the fish observed in the long net in Section 2.3.2.2.

3.3.1.9. The influence of the ration size on the size of the group at the feeding station

3.3.1.9.1. Introduction and methods

This experiment was designed to determine whether the ration level had an effect on the number of fish aggregating close at the feeding station.

On 23 May (day 37), at a temperature of 17°C, the 100% ration level was 1205 g of food per day. At 1700 on this day the ration was reduced to 10% of this level so that 30 g of food were delivered at each feed. All feeding times and video samples were carried out as normal after this period. The ration was increased again to an 100% level (1080 g) on 8 June (day 46). (It was kept at this level until day 105).

3.3.1.9.2. Results

After the ration was reduced there was a significant negative correlation (tau = -0.680; n = 26; $p < 0.001$) between the numbers counted at each feed and the number of the feed after reduction of the ration (Figure 3.13).

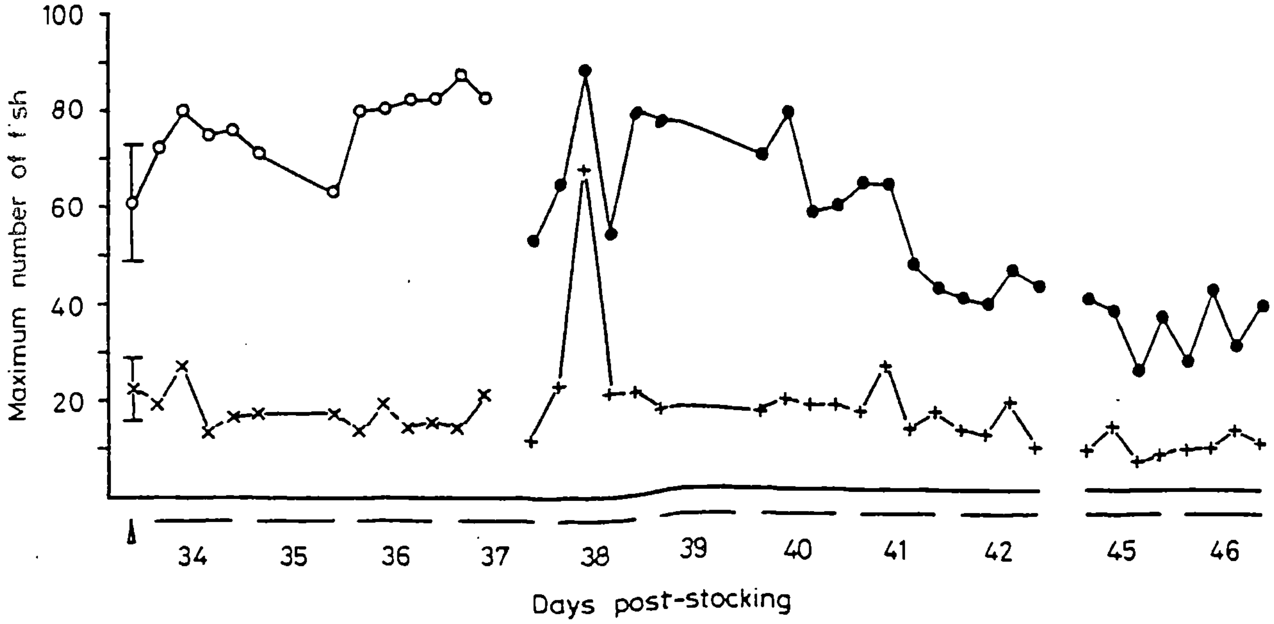


Figure 3.13. The effect of a 90% reduction in ration on the maximum number of fish seen feeding at the feeding station. Arrow shows the mean and standard deviation of maximum pre- and post-feeding numbers for days 14-33 (n = 34).

o represents the maximum number feeding per feed before the reduction.

● represents the maximum number feeding per feed after the reduction on day 37.

x represents the maximum pre-feeding number before the reduction.

+ represents the maximum pre-feeding number after the reduction on day 37.

During this period there was an increase in the anglers' catch rate (Section 3.3.4.2) suggesting that one of the effects of the reduction in ration was to promote a movement of some fish from the "forbidden" feeding area out into the available areas of the loch.

The reduction in numbers was accomplished by a decrease in the density of fish within the field of view which was shown by the significant correlation between the mean pre-trial number of the first of each pair of feeds and the number of the feed after the ration was reduced (tau = -0.743; n = 13; $p < 0.001$). The catchment area on the first of each pair of feeds was also calculated throughout the period of reduced rations using Method 1 of Section 3.3.1.6. There was no significant decrease in this area with feed number (tau = 0.0; n = 13; $p > 0.1$) and the mean of 81.72 m^2 (s.d. = 15.85; n = 13) was not significantly different from the mean of the period before the reduction (mean = 89.00 m^2; s.d. =29.34; n = 15) (t = 0.950; d.f. = 26; $p > 0.1$). There was also no significant change in the time at which different proportions of the group around the feeding station entered the field of view to feed (Table 3.3). These results strongly suggest that the effect of the change in ration size was not any change in the area occupied by the group around the feeding station but rather a reduction in the density of fish within this group.

There may be some error in counting maximum numbers as a result of fish arriving late and a flux of fish in and out of the field of view although even if fish did arrive later their behaviour would probably have gone unreinforced because all of the food was consumed in approximately 15 s (video and first hand observations). There was, however, no significant increase in the maximum number of fish counted on the second of each pair of feeds (Wilcoxon test; T = 17; N = 12; $p > 0.05$) suggesting either that no fish were attracted after the first feed or some were, but left the feeding area prior to the second feed.

After the ration had been increased to the 100% level again on day 46 the maximum number recorded feeding was only 42 on day 47. Unfortunately, the equipment was tampered with on day 51 and the experiment could not be continued to see if there was any subsequent increase in the numbers feeding. The experiment was, however, resumed on day 95 but only a maximum of 44 fish were recorded feeding and thus the numbers had not recovered to the level attained prior to reduction of the ration (even taking acount of those caught by angling). Whether this was a long term effect of the reduced ration or unrecorded angling during the intervening period could not be ascertained although it was most likely a result of the latter.

3.3.2. The behaviour of pre-conditioned rainbow trout with respect to a feeding station with a pre-feeding sound stimulus

3.3.2.1. Introduction and methods

The aim of the work described in this section was to attempt to attract pre-conditioned rainbow trout to the feeding station using a sound stimulus. Trout were pre-conditioned in Dunstaffnage Bay to move to a feeding station in response to an 140 Hz conditioned stimulus (Section 2.3.2.8.). After they were released into L. Charn a 1-min 140 Hz pulsed (2 s on; 0.5 s off) signal was played prior to each feed in an attempt to recall them. The reaction of the pre-conditioned fish to both sound and food was examined using UWTV and ultrasonic tags.

Prior to stocking with conditioned fish extensive angling was carried out around the feeding area (Section 3.3.4.) and after the stocking only one of the April stock was recaptured suggesting that the loch was virtually cleared of rainbow trout before this experiment.

3.3.2.2. Underwater television observations

3.3.2.2.1. Methods

The methods were the same as those described in Section 3.3.1. except that a 6-min video sample was recorded at each feed; 2.5 min before the sound signal until 2.5 min after the feed. Analysis was also the same as Section 3.3.1. with the counts being taken every 10 s during the samples and the maximum number of fish in view being recorded for each sample.

3.3.2.2.2. General observations

Figure 3.14 shows that there was an initial increase in the number of fish which parallels the observations recorded in Section 3.3.2. Unlike this earlier section, however, there was no long term improvement in the response and from day 12 onwards only transient appearances were recorded which suggests that, although fish were not aggregating around the feeding station, some were feeding outside of this area. Video observations between feeds showed that larger numbers of fish frequented the area at other times as, for example, on day 22, 24 fish were counted in the field of view 51 min after the 1600 feed. No consistent relationship between the timing of these maxima could be established to enable the timing of the feed to be improved to observe more fish.

The main reasons for this contrasting result were weather conditions and the presence of a predator. Stronger winds were experienced throughout this experiment with the result that food was often spread over a wide area soon after feeding. Fish were therefore not reinforced in the same position and so would have been less likely to aggregate close to the feeder. Throughout this experiment a cormorant, *Phalacrocorax carbo*, was regularly seen at the loch and, as it was recorded below the feeding station during a feeding time video sample and is known to prey on salmonids (Mills, 1965), it was probably also responsible for the decline in the number of fish remaining close to the feeding station. In addition, decreasing water temperatures may have reduced the motivation to feed. All of these factors would have been detrimental to the development of both the response to the feeding station and the conditioned response.

3.3.2.2.3. Observations of the conditioned response

Figure 3.14 shows that there was no significant long term improvement in the conditioned response. This, initially at least, may have been because the fish reacted outside of the field of view, were unable to respond directionally to the sound stimulus or were unable to respond because they were in a visually unfamiliar environment. They may also have lost their conditioning and to check that fish were still conditioned the loudspeaker was raised to 60 cm and placed in a black plastic cover, as it had been in Dunstaffnage Bay, from day 2 to day 6.

With the loudspeaker in its shallower position some positive reactions to the sound signal were observed which resulted in a general increase in activity within the field of view. There was also some weak circling of fish around the transducer which, although not as vigorous as it had been in Dunstaffnage Bay, suggested that the fish had not lost their conditioning. On day 2 and day 3 these responses resulted in a significant increase in the maximum number seen during the sound signal when compared with the maximum number seen in the 2.5-min period immediately preceeding it (Wilcoxon test; $T = 4$; $N = 8$; $p = 0.05$). The mean difference was, however, small (3.0; range -2 to + 9), inconsistent in the long term and the number feeding was always greater (Figure 3.14). On several occasions fish were known to be active within the feeding area (judging by the occasional rise) but could not be attracted into the field of view and thus the television observations provided no evidence of any significant attraction. There were, however, disadvantages in using the camera because it had a very limited field of view and could not record any attraction that may

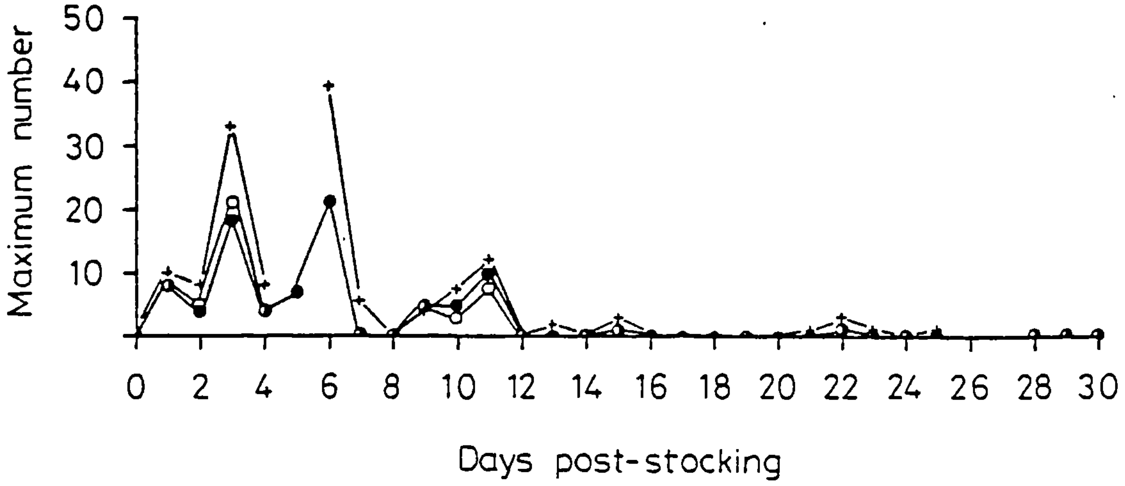


Figure 3.14. A summary of the video observations made at the feeding station between 12 September and 12 October 1980. Each point represents the mean of the maximum number seen for 2.5 min before the conditioned stimulus (●), the maximum number seen during the 1 min stimulus (o) * and the maximum number seen in the 2.5 min after feeding (+). On days 1, 6 and 20 there was no conditioned stimulus before feeding and on day 5 there was no conditioned stimulus or food.

* (the stimulus duration was extended to 5 min during some of the ultrasonic tagging experiments but this increased duration did not significantly improve the response on any occasion)

have taken place over a wider area. Consequently, most conclusions on the reaction of the pre-conditioned fish had to be made from the ultrasonically tagged fish although the data is necessarily limited to only four fish.

Video observations were continued until 31 October. On 22 October, 150 unconditioned rainbow trout were introduced into the loch in an attempt to improve the response but, after an initial increase in the numbers counted feeding at the feeding station, the numbers were again reduced to zero at each feed. The experiment was therefore stopped on 31 October.

3.3.2.3. Observations on the rising of rainbow trout to artificial food

These observations were very limited in this experiment because of the need to track ultrasonically tagged fish at the same time. A variable number of rises were, however, consistently observed throughout the experiment although there was no increase in the maximum number of rises or decrease in the time taken to reach this peak as there had been in the previous experiment (Section 3.3.1.2.). Even though there were occasionally a large number of fish rising in the feeding area fish were also observed rising to hand thrown pellets in other parts of the loch (NNE shallow end, in particular) within one hour of feeding time suggesting that not all the fish were attracted to the feeder.

3.3.2.4. The movements of ultrasonically tagged rainbow trout between feeding times

3.3.2.4.1. The movements of fishes F1 and S1 on days 0 to 2

Both fish covered large areas of the loch after release (Figure 3.15). The occasionally quick movement and high ambient noise as a result of rain sometimes made it difficult to obtain simultaneous fixes with the two hydrophones. When this happened, and where it was obvious that a major excursion had been made, the approximate position of the fish was plotted on

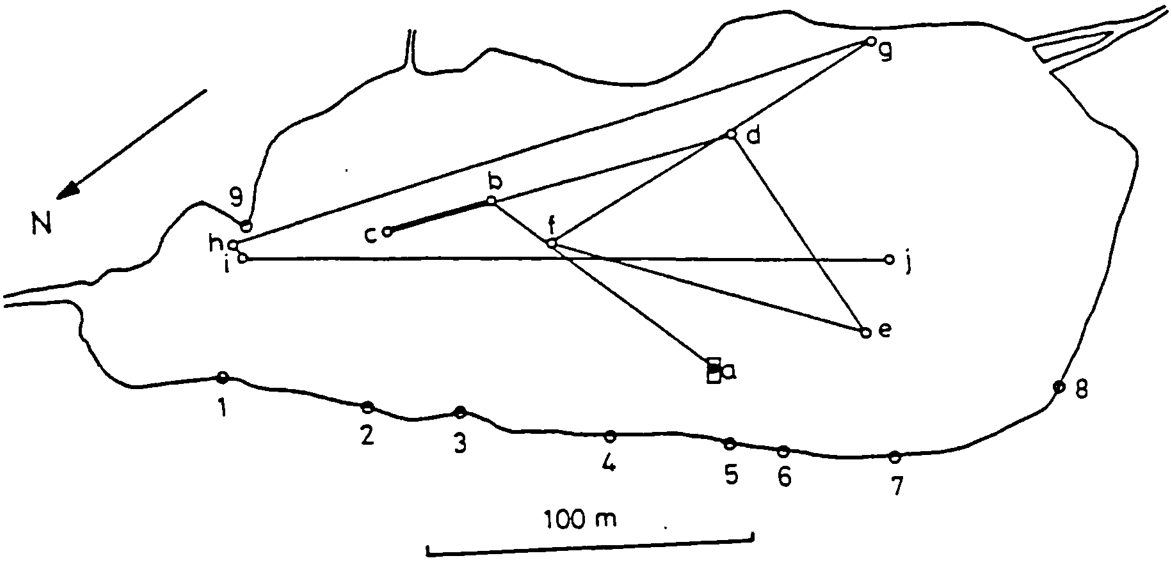
Figure 3.15. Immediate post-stocking movements of fishes S1 (a) and F1 (b) after release from the feeding station.

The fish were located, at the positions indicated, at the following times :

(a) Fish S1 :	(b) Fish F1 :
a. 1340	a. 1340
b. 1350	b. 1355
c. 1415 * from 2	c. 1447 * from 3
d. 1454	d. 1454 * from 4
e. 1503	e. 1455
f. 1508 * from 4	f. 1503
g. 1509	g. 1521
h. 1630	h. 1604
i. 1637	i. 1655
j. 1756 * from 6	j. 1751

* represents a single fix obtained from the station indicated.

(a)



(b)

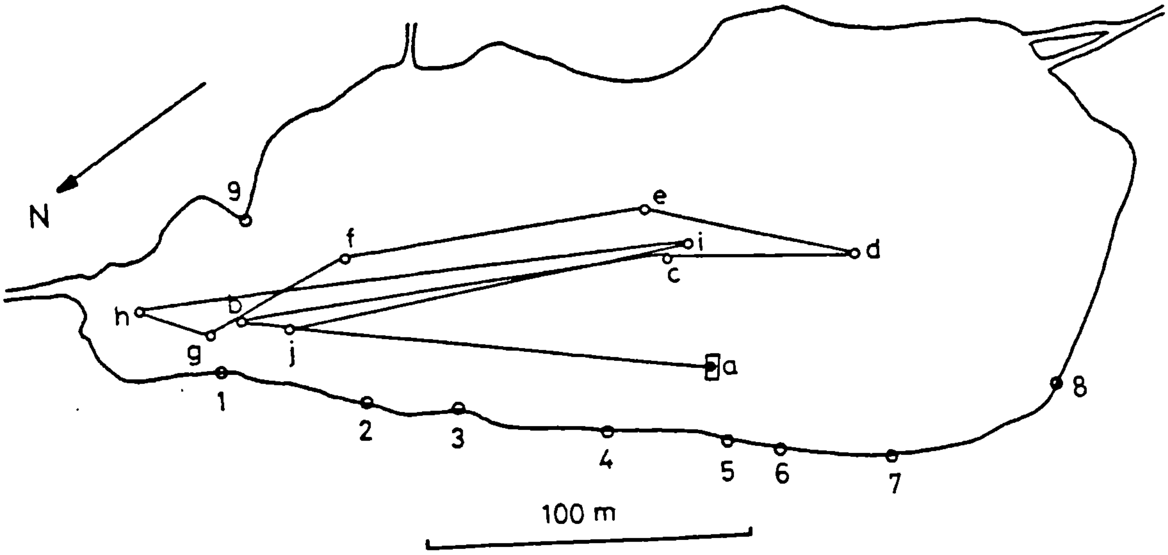


Figure 3.15, and all subsequent figures, from the bearing and an approximation based on the signal strength. Where this procedure was used an asterisk is marked in the legend next to the appropriate fix along with the number of the shore station from which the fix was obtained.

After release both fish moved away from the feeder in a north easterly direction and it may be significant that there was a strong wind (Beaufort scale; Force 7) blowing in this direction during the sampling period. This wind would probably have generated surface currents, which may promote downwind movement (Thorpe et al., 1981), although subsequent movement was not confined to this direction as both fish subsequently made extensive excursions throughout the loch.

On day 1 there was contrastingly less movement than there had been the previous day (Figure 3.16) with both fish showing a preference for the shallow north-north-eastern end of the loch. Fish F1 was initially located in the feeding area where it appeared to be feeding along with some other fish that were rising to food which had probably been delivered on the previous 0915 feed. It then moved to the eastern shore and subsequently to the shallow end where it remained until 1727 when it again moved to the feeding station to feed (Section 3.3.2.5.1.). Fish S1 was restricted in its activity to the shallow end of the loch throughout all of the sampling period (up to 1821) which was also a marked contrast to its behaviour of the previous day.

On day 2, fish F1 again showed a preference for the NNE end and although fish S1 was only spasmodically located it also spent some time in this area (Figure 3.17). At the start of the sampling period, F1 was probably disturbed as it made a long excursion from the shallow end before eventually returning and spending most of the sampling period within this area prior to moving to the feeding station at 1810. There was some visible feeding on natural surface food here between 1350 and 1415 which may have helped keep the fish in this area.

Figure 3.16. Movements of fishes S1 (a) and F1 (b) on day 1.

The fish were located, at the positions indicated, at the following times :

(a) Fish S1 :

a. 1105 * from 1

b. 1136

c. 1140

d. 1159

e. 1219

f. 1224

g. 1243, 1341, 1440 * from 1

h. 1500, 1573, 1613 * from 1

i. 1747

h. 1821

(b) Fish F1 :

a. 1105

b. 1110

c. 1204

d. 1211

e. 1230

f. 1234 * from 4

g. 1241 * from 2

h. 1243 * from 1

i. 1329 * from 1

j. 1333

k. 1245,1440 * from 1.

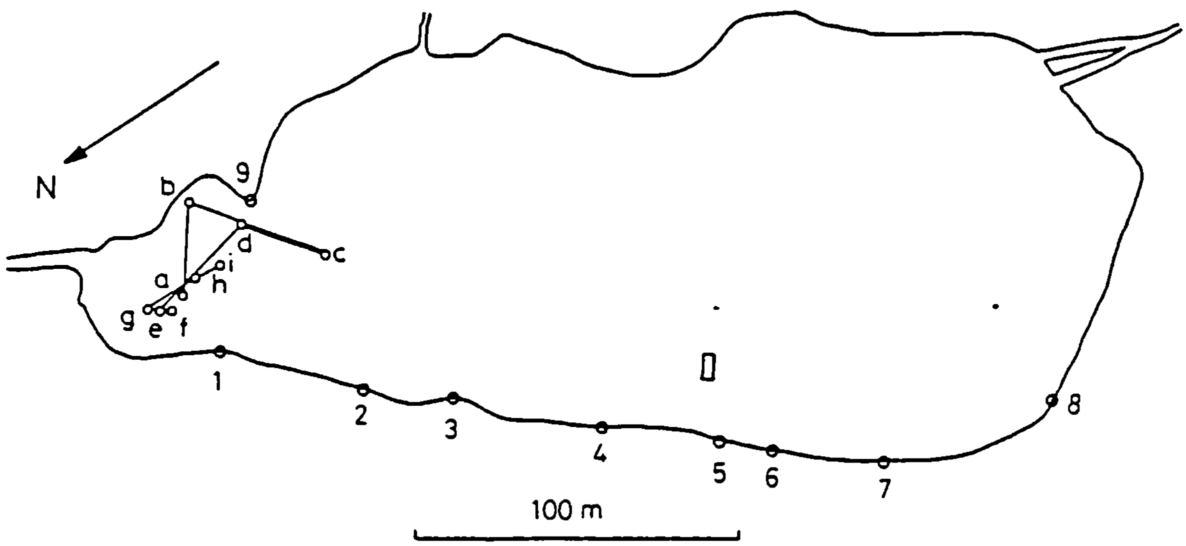
l. 1500, 1537

m. 1613

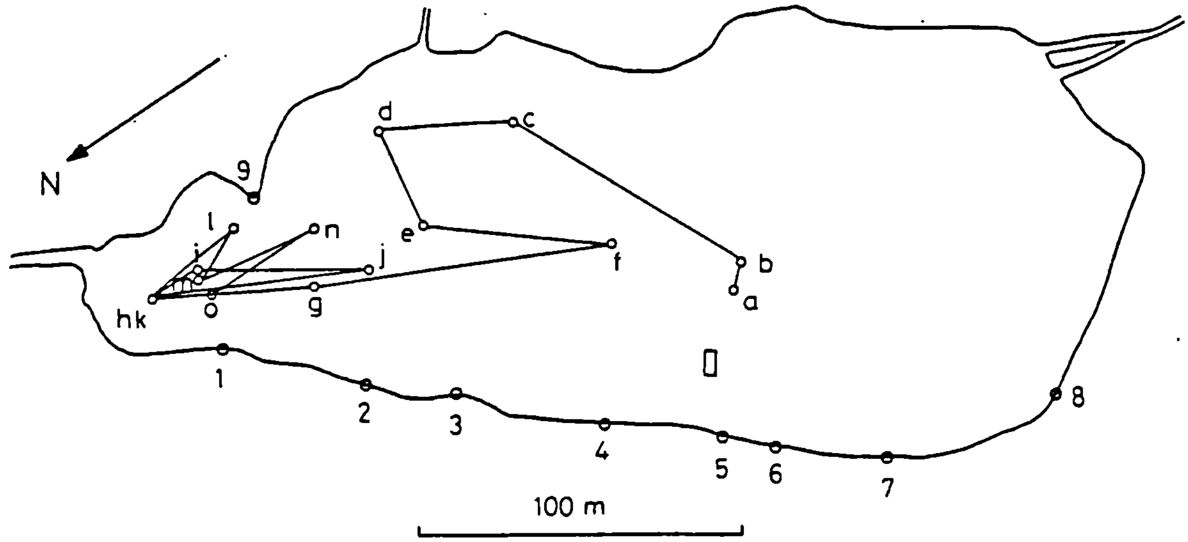
n. 1658, 1718

o. 1727

(a)


N
b
9
d
c
i
a
h
g
e
f
1
2
3
4
5
6
7
8
100 m

(b)


N
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4
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6
7
8
100 m

Figure 3.17. Movement of fishes S1 (a) and F1 (b) on day 2.

The fish were located, at the positions indicated, at the following times :

(a) Fish S1 :

a. 1255

b. 1319

c. 1354

d. 1415

1434 contact lost

(b) Fish F1 :

a. 1119

b. 1135 * from 6

c. 1159

d. 1203

e. 1215 * from 1

f. 1218 * from 1

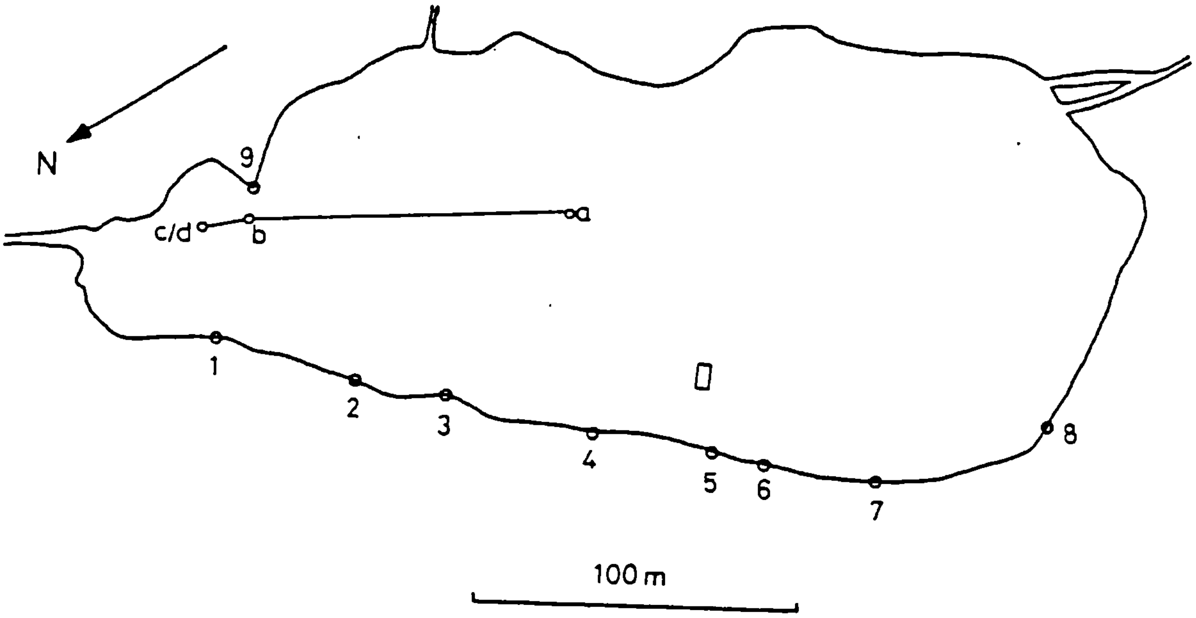
g. 1305 * from 1

h. 1341 * from 1

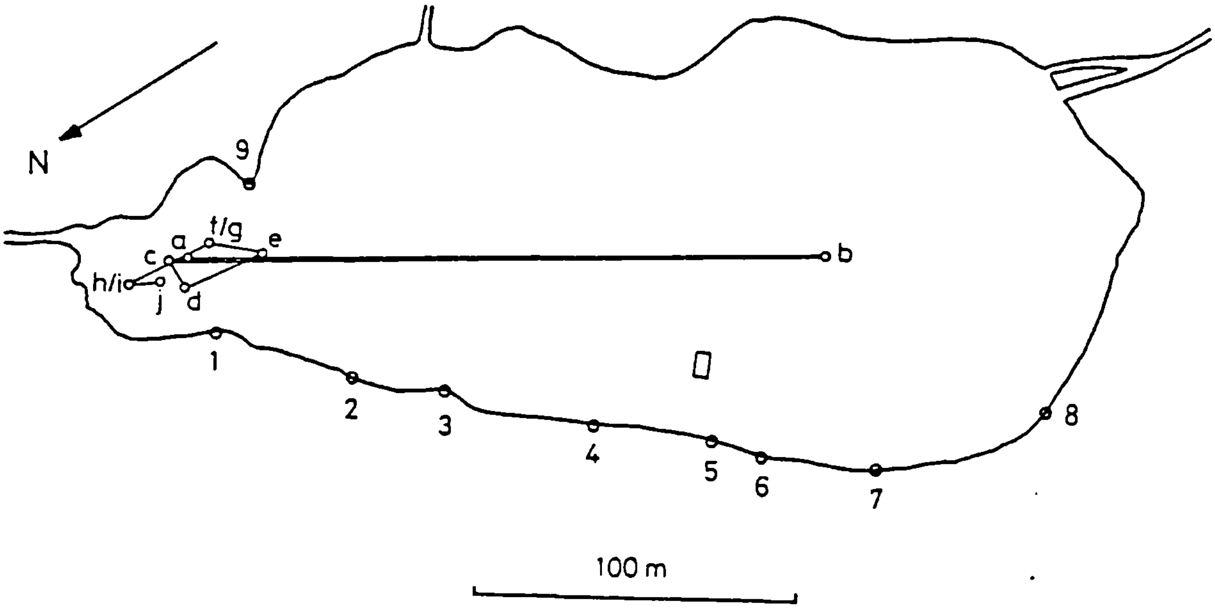
i. 1451

j. 1545 * from 1

(a)



(b)



Initially, S1 could not be located from the bank although at 1255 it was located from a boat in the centre of the loch. It then moved to the shallow end but was subsequently lost. No further days data was obtained from either fish as a result of premature tag failure.

In summary, both fish made extensive post-stocking movements but were less active on subsequent days when they showed a preference for the north-north-eastern end of the loch.

3.3.2.4.2. The movements of fishes F2 and S2 on days 10 to 29

3.3.2.4.2.1. Introduction and methods

Both of these fish were tracked for considerably longer than the first pair (F1, S1). During this period there was an obvious shift in the preferred position of both fish. This change was quantified according to the methods of Hayne (1949), Harrison (1958) and White (1964) adopted by Holliday *et al.* (1974).

First, the loch was divided into a grid composed of 25 m x 25 m squares. Fixes, which were taken at intervals ranging from a minimum of one every 15 min to a maximum of one every 5 min, were assumed to lie in the centre of each particular square and then expressed as an x and y co-ordinate within the total grid. The 'centre of activity' (Hayne, 1949) is the mean of all these x and y values, which were taken between feeding times on each day, and represents the centre of the animals preferred area on that particular day.

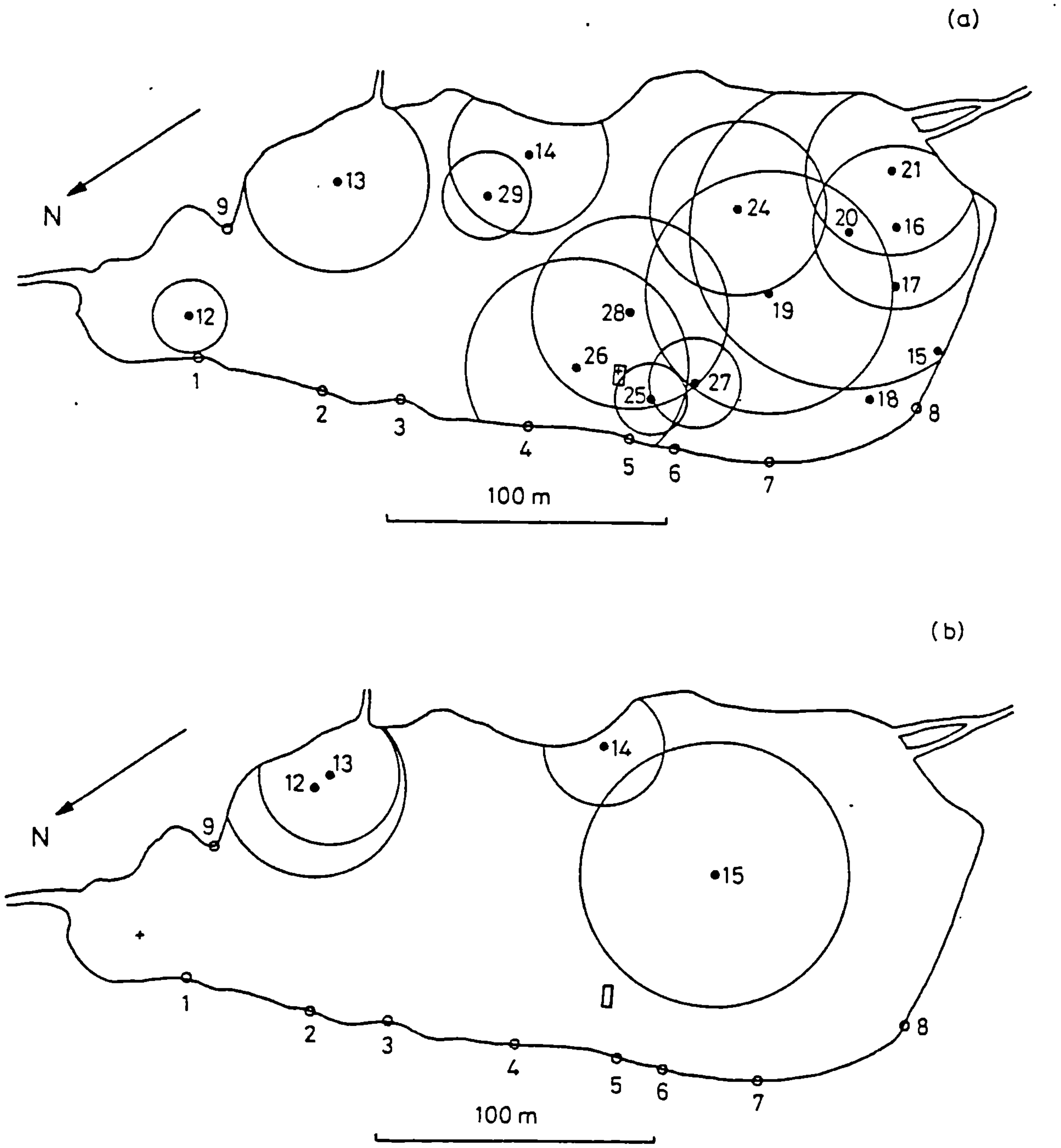
An index of the range of activity was also calculated according to the method of Harrison (1958) and White (1964). This index is the standard deviation of the distance of each positional fix from the centre of activity and represents a statistical area in which the fish spends 68.3% of its time.

3.3.2.4.2.2. Results

Figures 3.18a and 3.18b show that both fish exhibited a long term shift in their daily preferred areas. The pattern of movement was in no way correlated

Figure 3.18. Daily changes in the centre of activity of ultrasonically tagged rainbow trout S2 (a) and F2 (b). Each point represents the centre of activity on the designated day post-stocking. The circle around each point represents the index of range of activity which is the area in which the fish spends 68.3% of its time. + represents the point of capture and release between 1800 and 1830 on day 10. The sampling periods and number of fixes (n) used to construct the centre of activity and index of range activity are shown below :

Sampling periods for S2	Sampling periods for F2
Day 12; 1450-1607; n = 8	Day 12; 1450-1607; n = 7
Day 13; 1206-1500; n = 8	Day 13; 1206-1500; n = 12
Day 14; 0945-1237; n = 11	Day 14; 0945-1237; n = 12
Day 15; 1456-1613; n = 7	Day 15; 1451-1611; n = 5
Day 16; 1455-1606; n = 6	
Day 17; 1426 - located then disturbed	
Day 18; 1436 - located then disturbed	
Day 19; 1440-1600; n = 11	
Day 20; 1030-1600; n = 69	
Day 21; 1530-1600; n = 4	
Day 22 - Day 23;no data	
Day 24; 1536-1600; n = 5	
Day 25; 1444-1550; n = 8	
Day 26; 0955-1615; n = 30	
Day 27; 1525-1700; n = 9	
Day 28; 1500-1700; n = 14	
Day 29; 1535-1600; n = 6	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(b)
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with the positions at which the fish were initially captured during feeding (1800) on day 10, suggesting that on this occasion, even 10 days after stocking, there was no fixed distribution of fish within the loch.

Fish F2 showed no preference for its release point at the feeder and was located on the eastern shore from day 12 - day 14 (Figure 3.18b). It was lost on day 15. Fish S2 moved towards to the southern end of the loch from day 12 to day 15 and from day 16 to day 24 it was consistently located at this end (Figure 3.18b). If this fish could not be located from stations 1-7 during this latter period it was invariably located close in to the southern shore where, because it was shallow and muddy, the signal was severely attenuated making reception difficult unless the hydrophone was close to the fish. On these occasions this fish was sometimes disturbed and where this had obviously happened only the initial position was marked on Figure 3.18 (e.g. fish S2; day 17, 18).

From day 25 until day 28, fish S2 was consistently located within the feeding area (Figure 3.18a). This movement represents a shift into the area of the loch where food is locally most abundant and may be analogous to, although less localized than, the aggregation around the feeding station found after the April stocking (Section 3.3.1.).

There was a large variation in the activity of individual fish between individual days which is reflected in the variation in the index of range activity (Figure 3.18). This variation may have been due to variations in stomach fullness as fish may be less active with a full stomach (Holliday et al., 1974), although there was no correlation between a fish feeding at the feeding station and later activity. Activity may also have been affected by the presence of the cormorant (although this bird usually left the loch when humans were there) and interactions with other fish. In particular, the presence of other actively feeding fish may have stimulated activity as, for example, on day 20 when fish S2 was active throughout large areas of the loch (Figure 3.19). On this occasion

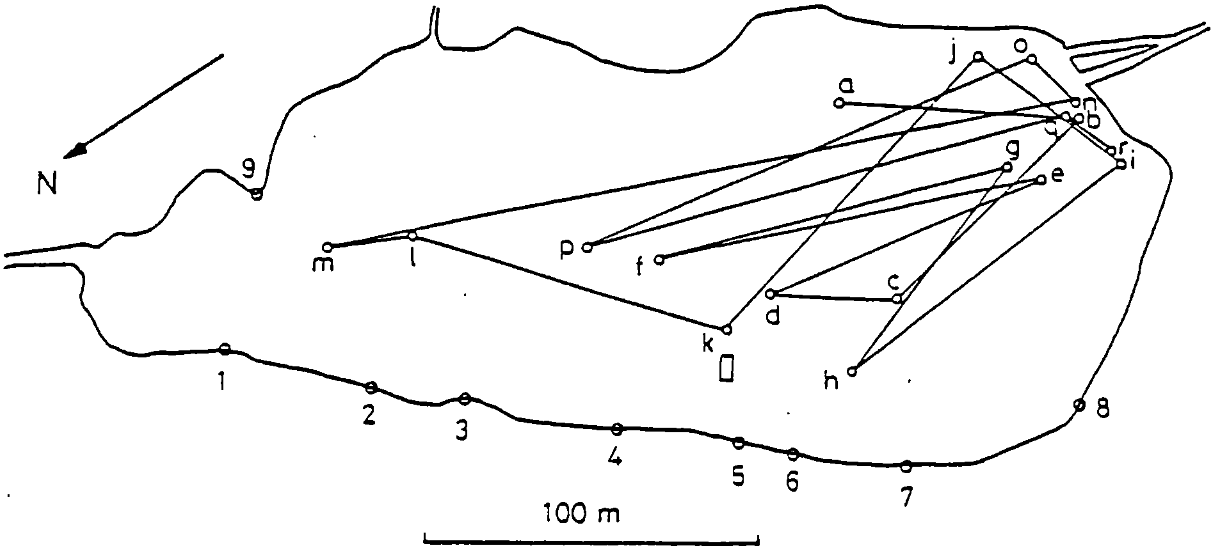


Figure 3.19. Movements of fish S2 before the food was delivered on day 20. The fish was located, at the positions indicated, at the following times :

a. 1029

b. 1035

c. 1045

d. 1100

e. 1110

f. 1130 * from 4

g. 1140

h. 1145

i. 1206

j. 1230

k. 1245

l. 1258

m. 1300 * from 2

n. 1316, 1400

o. 1430

p. 1434 * from 5

q. 1145, 1535

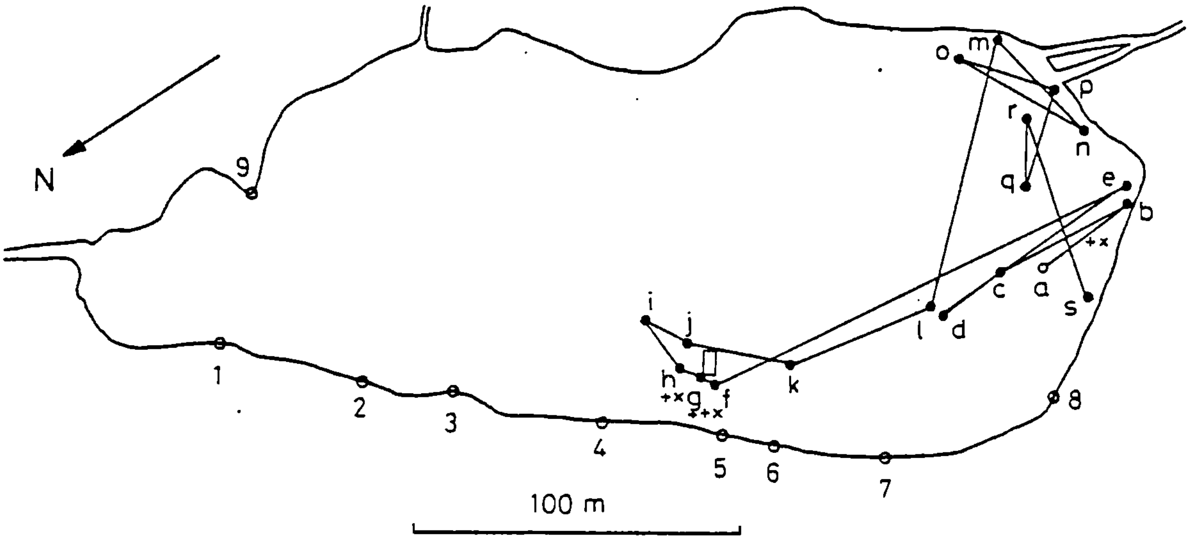
r. 1545

Figure 3.20. Movements of fish S2 before and after feeding on day 17. The approximate position of the fish when the conditioned stimulus started (x) and when food was delivered (+) is marked on the map at the relevant position. Blackened circles show the fixes taken after the food delivery.

The fish was located, at the positions indicated, at the following times :

a. 1430
  1600 - conditioned stimulus on (+)
  1601 - food delivered (x)
  1609 - other fish start feeding
      at the feeding station
b. 1611
c. 1627
d. 1630
e. 1634
f. 1640
  1645 - conditioned stimulus on (+)
  1647 - conditioned stimulus on (+)
  1648 - food delivered (x)
g. 1700
  1721 - conditioned stimulus on (+)
  1722 - food delivered (x)

h. 1730
i. 1739
j. 1750
k. 1810
l. 1825
m. 1830
n. 1840
o. 1900
p. 1915
q. 1920
r. 1945
s. 1950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other fish were rising to pellets remaining from the previous feed and the tagged fish was located with these fish in the feeding area as well as covering other areas of the loch.

Human disturbance may also have influenced activity and on days 17 and 18, when fish S2 was disturbed during location, it made extensive forays into the loch. On day 17, the fish moved towards the feeding station even though there was no visible feeding activity within this area and this suggested that the fish may have become conditioned to associate human disturbance with feeding opportunities nearer the feeding station.

From day 15 until day 24, fish S2, which was consistently located at the southern end of the loch at this time (Figure 3.18a), was recorded feeding at the feeding station on 6 out of the 9 observed feeding times. This result suggests that it fed at the feeder but returned to its 'preferred area' after feeding and this behaviour was confirmed on day 17 (Figure 3.20).

3.3.2.5. The attraction of ultrasonically tagged fish to the feeding station

3.3.2.5.1. The attraction of fishes F1 and S1 on days 0 to 2.

After they were released into the loch on day 0 both ultrasonically tagged fish were located and probably feeding at the feeder 25 min after the food was delivered at 1805. This attraction lacks an adequate pre-trial control period, however, because both fish were very active throughout the loch prior to the feed.

As a control measure, on day 1, no sound signal preceeded the evening feeds at 1600 and 1700. There was an adequate pre-feeding control period as both fish had been inactive in the shallow north-north-eastern end of the loch since 1230 (Figure 3.16). There was no immediate reaction to the 1600 feed (Figure 3.21), but a delayed reaction with fish F1 disappearing from the shallow NNE end at 1747 and arriving at the feeding station at 1753. Fish S1 showed no

Figure 3.21. The reaction of fish F1 to a food delivery, without a sound stimulus, on day 1 showing movements before (o) and after the delivery (●). Figure 3.16 shows more extensive pre-feeding data for this fish.

The fish was located, at the positions indicated, at the following times :

a. 1440

b. 1500, 1537

1600 - food delivered (x); other fish immediately rising to food at the feeding station

c. 1613

d. 1658

1700 - food delivered (x)

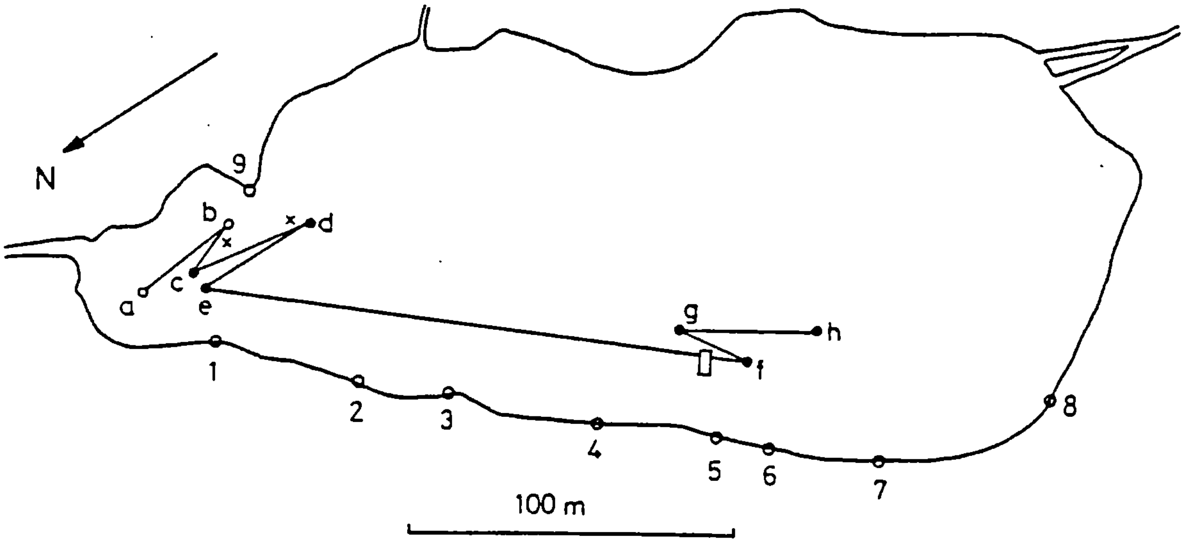
e. 1718, 1727, 1747

1748 - fish moved away from e. in a south-westerly direction

f. 1753 - fish located close to other feeding fish

g. 1756

h. 1811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noticeable reaction and remained at this end of the loch throughout the sampling period. In the time interval between the initial 1600 feed and this net movement towards the feeding area there was considerable feeding activity near the feeder and this localized activity was probably responsible for the appearance of the fish close to the feeder at 1753. The exact pathway which the fish took towards the feeding area was not observed, but appeared to be indirect rather than direct as it was only located at the feeder 6 min after leaving the NNE end of the loch. There were no pellets drifting into the NNE end from the feeder when the fish moved away from this area. Consequently the presence of food did not initiate the observed bout of activity and this result suggests that fish could be attracted to the feeding area without a pre-feeding conditioned stimulus via the stimulus of unknown feeding cues.

On day 2, fish F1 was inactive in the shallow NNE end for 6 h preceeding the feed. On this occasion a 1-min pre-feeding sound stimulus followed by a food delivery was given at 1609. This feed was proceeded by a net movement out of the shallow area at 1610 followed at 1640 by the arrival of the fish at the feeding station (Figure 3.22a). This result suggested that the sound signal was responsible for the movement but that the 1-min signal was not long enough to attract the fish to the feeding point and final location was accomplished using cues from fish feeding nearer the feeding station. Measurements of sound propagation in the loch (Section 3.3.2.7.), however, showed that the signal was inaudible in the position at which F1 was located at 1609 and it is therefore unlikely that this fish heard the conditioned stimulus. It is possible that it reacted quickly because fish further away had reacted to the signal and this somehow stimulated its own activity. It is also possible that human disturbance may have initiated the reaction, although positions were fixed from the same places on the bank throughout the day and no such reaction was recorded during these periods.

Figure 3.22. The reaction of stationary (a) and active (b) fish to the conditioned stimulus (+) and a food delivery (x).

Figure 3.17 shows more extensive pre-feeding data for fish F1.

The fish were located, at the positions indicated, at the following times :

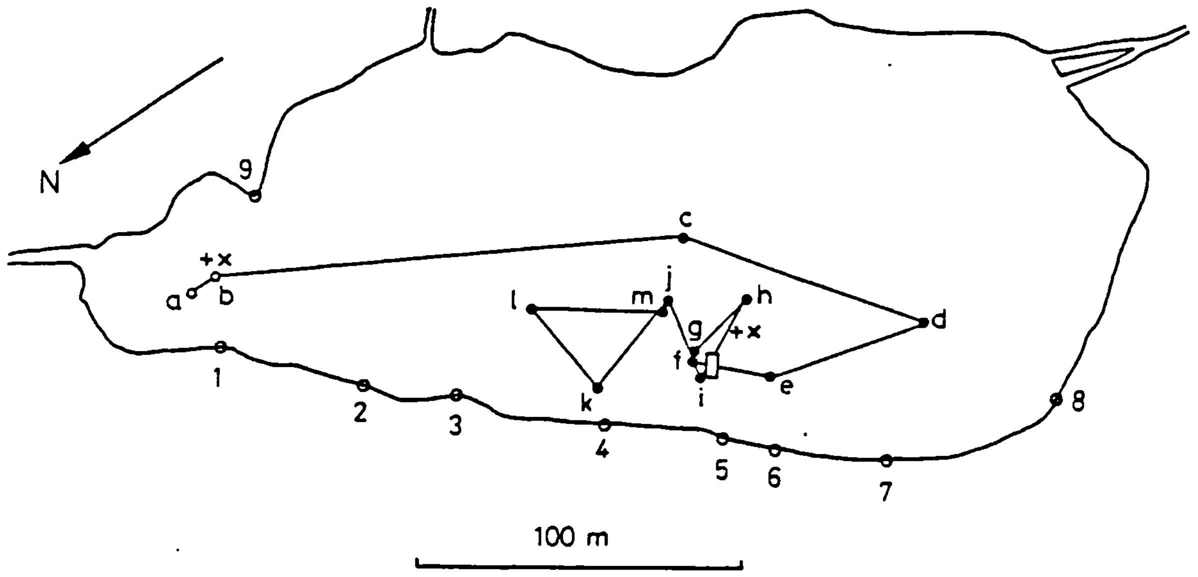
(a) Fish F1 (day 2)

a. 1600
b. 1608
    1609 - conditioning stimulus on (+)
    1610 - food delivered (x); other fish immediately start feeding at the feeding station
    1610 - fish lost from Station 1
c. 1616
d. 1632 * from 6
e. 1637 - located with other feeding fish from this time until 1817
f. 1640
g. 1650
h. 1708
    1715 - conditioned stimulus on (+)
    1716 - food delivered (x)
i. 1728
j. 1756
k. 1805
l. 1807
m. 1817

(b) Fish F2 (day 15)

a. 1454
b. 1508
c. 1550
d. 1608
e. 1611
    1613 - conditioned stimulus on (+)
    1624 food delivered (x)
f. 1615 - conditioned stimulus on (+)
g. 1617
h. 1619
i. 1621
j. 1622
    1623 - conditioned stimulus on (+)
    1624 - food delivered on (x)
k. 1625
l. 1626 * from 1
    1628 - other fish start feeding at the feeding station
m. 1640
n. 1642
o. 1649 - feeding in the feeding area with other fish until observations were stopped at 1837.

(a)



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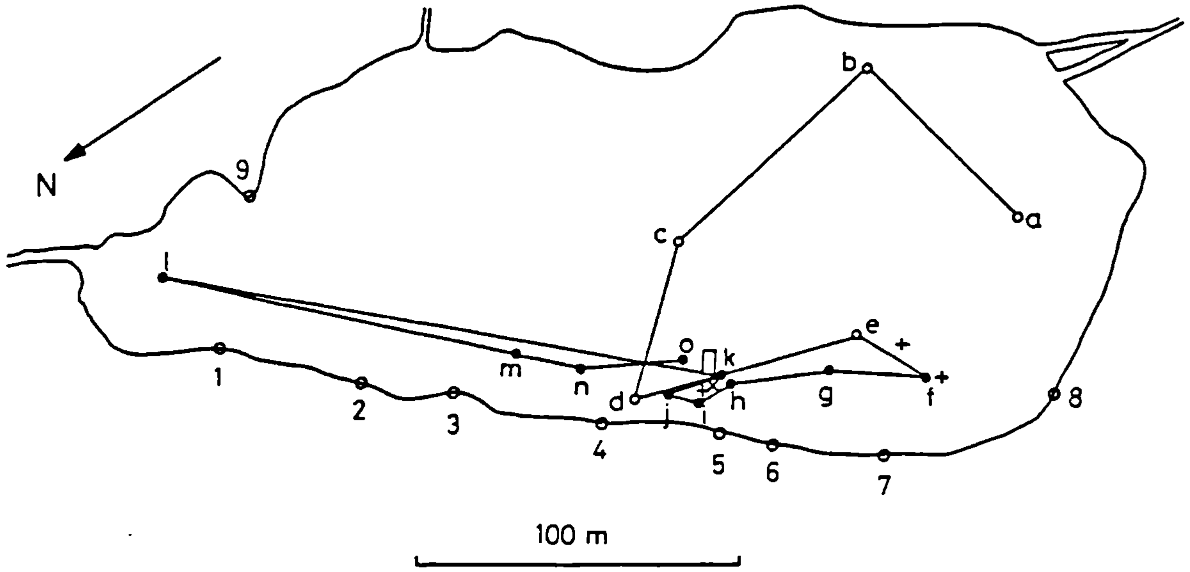
(b)



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100 m

In summary, it appeared from these initial observations that fish could be attracted to feed at the feeder both in the presence and absence of a pre-feeding sound stimulus. Further experiments with the next two fish (F2 and S2), were designed to help clarify the situation.

3.3.2.5.2. The attraction of fishes F2 and S2 on days 10 to 29

3.3.2.5.2.1. The reaction to the sound stimulus

An unequivocal reaction to the conditioned stimulus was never demonstrated with these two fish. Signals of up to 5 min duration, without feeding, were used when the fish was in a "receptive area" (sound pressure > 0 dB// 1μbar at 1 m depth; Section 3.3.2.7.) so there was ample time to react. On no occasion was there any noticeable, immediate reaction to the sound signal when the fish were inactive or localized in their pre-trial behaviour (e.g. Figure 3.25). When fish were active and accurate fixes were taken immediately before and after the onset of the sound signal, possible positive movement towards the feeder was recorded on four occasions (e.g. Figure 3.22b) although, as two null and three negative reactions were recorded on similar occasions, the results could have arisen by chance. The sound signal may, however, have promoted some activity and it is possible that more sensitive telemetry equipment could have detected some reaction. Even though only gross reactions could be detected with the system used, however, such gross movements were required and different equipment would probably not have altered the conclusion of this section. In summary, this was that tagged fish were not attracted to the feeding station by the conditioned stimulus.

3.3.2.5.2.2. The reaction to the stimulus of food

Although no unequivocal reaction to the sound stimulus could be demonstrated, there was ample evidence that fish were attracted from anywhere in the loch, to the feeding station, after food had been delivered at the feeding station. Of the 24 pairs of feeds during which fishes F2 and S2 were tracked, one fish fed at the feeding station on 15 occasions independently of its original position. The fact that the fish fed, but did not react to the sound stimulus, suggests that the lack of reaction to the sound stimulus was not due to any lack of feeding motivation.

The typical reaction to a food delivery is exemplified by the reaction of fish F1 to feeding in Section 3.3.2.5.1. (Figure 3.21). On other occasions there was a variable delayed reaction before the fish moved to the feeding station (e.g. Figure 3.23). Tagged fish took variable and erratic pathways to the feeding area which appeared to be highly dependent on the distribution of pellets and the position of other feeding fish in the loch (Section 3.3.2.6.). The fish were certainly feeding during these excursions as they were often located at the feeding station and with other feeding fish.

Because the fish were always fed at a similar time they may have anticipated feeding time (Section 3.3.1.8.) and therefore the reactions may not have been related to any cues coming from the actual feed itself. This spontaneous activity would not have occurred on the first day after stocking, however, (Figure 2.21) and on two days when the start of the evening feed was delayed until 1700 there was no spontaneous activity during the intervening period. Therefore, although the results do not entirely eliminate the use of a time co-ordinated cue, it is considered unlikely to be responsible for all the observed reactions.

The tagged fish were usually only attracted when other fish were actively feeding at the feeding station or in other areas of the loch. On one occasion fish S2 was attracted from the north-eastern shore to feed at the feeder but it was later discovered that pellets had blown into this area prior to its movement. Thus, although on some occasions food may have promoted movement and must have been responsible for stimulating fish close to the

Figure 3.23. The reaction of fish S2 to a food delivery on day 20 and its reaction to food blown over a wide area by the wind blowing at Force 3 in the approximate direction W.

The fish was located , at the positions indicated, at the following times :

a. 1430

b. 1434 * from 5

c. 1445, 1535

d. 1538, 1545

1558 - conditioned stimulus on (+)

1600 "

1602 "

1603 "

1605 "

1606 - food delivered (x)

1607 - other fish start feeding
feeding at the feeding station

e. 1610

f. 1614

g. 1618

h. 1620

i. 1621

j. 1622

k. 1625

l. 1627 - fish located with
other feeding fish
until 1655

m. 1630

n. 1634

o. 1640

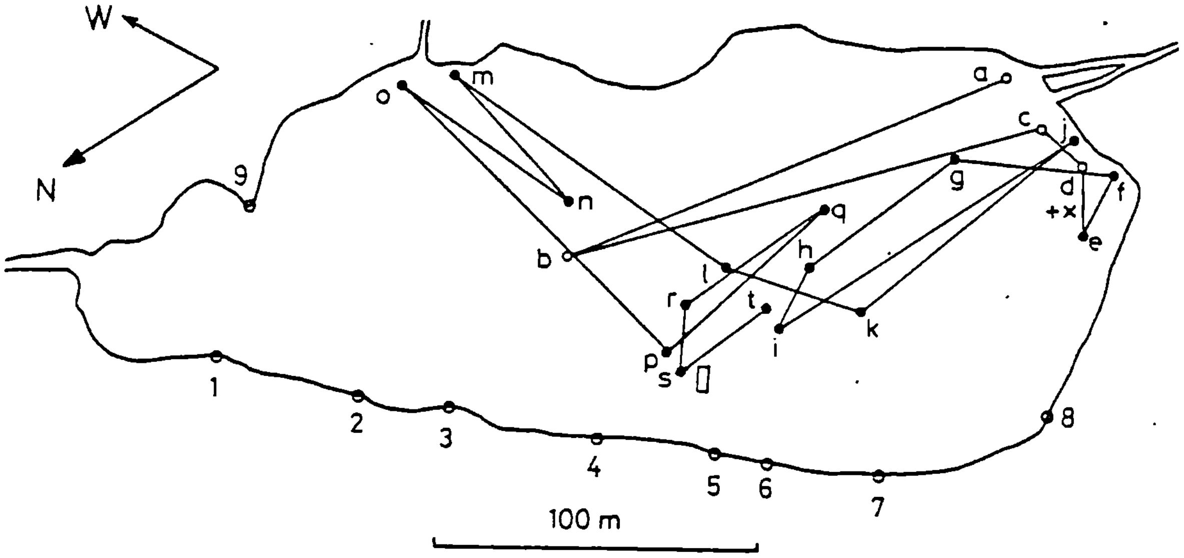
p. 1646

q. 1647

r. 1653

s. 1654

t. 1655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feeder, the presence of other feeding fish was probably of prime importance in stimulating activity in most instances.

3.3.2.6. Observations on the movements of tagged rainbow trout during feeding

The movements of rainbow trout once they had been stimulated to approach the feeder were primarily determined by the distribution of pellets around the loch and revealed how prey distribution could influence feeding excursions in this species. Two contrasting patterns of movement were observed when the pellets were wind blown over a wide area and when they were only distributed closer to the feeder on calmer days.

Figures 3.23 and 3.24 illustrate the movements of an ultrasonically tagged fish in response to pellets blown by the wind in two different directions. On these occasions the tagged fish was located moving up and down the area over which wind blown pellets were heading which suggests that the behaviour was not habitual but primarily related to the food distribution. These fish were definitely feeding on the pellets during these excursions because several times they were located with other actively feeding groups. On several occasions after the fish had fed over a wider area, they moved towards the source of the food (e.g. Figure 3.23) and this type of behaviour may have been responsible for the increase in the numbers counted on the video after feeding in the first experiment (Section 3.3.1.3. Figure 3.7).

When food was more limited in its distribution, fish were more localised in their habits (Figure 3.25), although they sometimes made excursions away from the feeding area on these occasions, perhaps to search other areas for food.

At times other than feeding times, ultrasonically tagged fish were occasionally located away from the feeding area with other groups of fish that were milling near the surface. In addition, the tagged fish were often located

Figure 3.24. The reaction of fish S2, on day 29, to food blown over a wide area by the wind blowing at Force 4/5 in the approximate direction W.

The fish was located, at the positions indicated, at the following times :

a. 1535
b. 1540
c. 1550
d. 1600
  1600 - conditioned stimulus on (+)
  1601 - food delivered (x)
  1605 - other fish start
  feeding at the feeding station
e. 1610
f. 1615
g. 1620
f. 1655
g. 1620

f. 1655
h. 1705 - fish located near other
  feeding fish at the southern
  end of the loch
i. 1710
j. 1715
k. 1725
l. 1730, 1740 - feeding near
  the feeding station until 1830
m. 1800
n. 1830

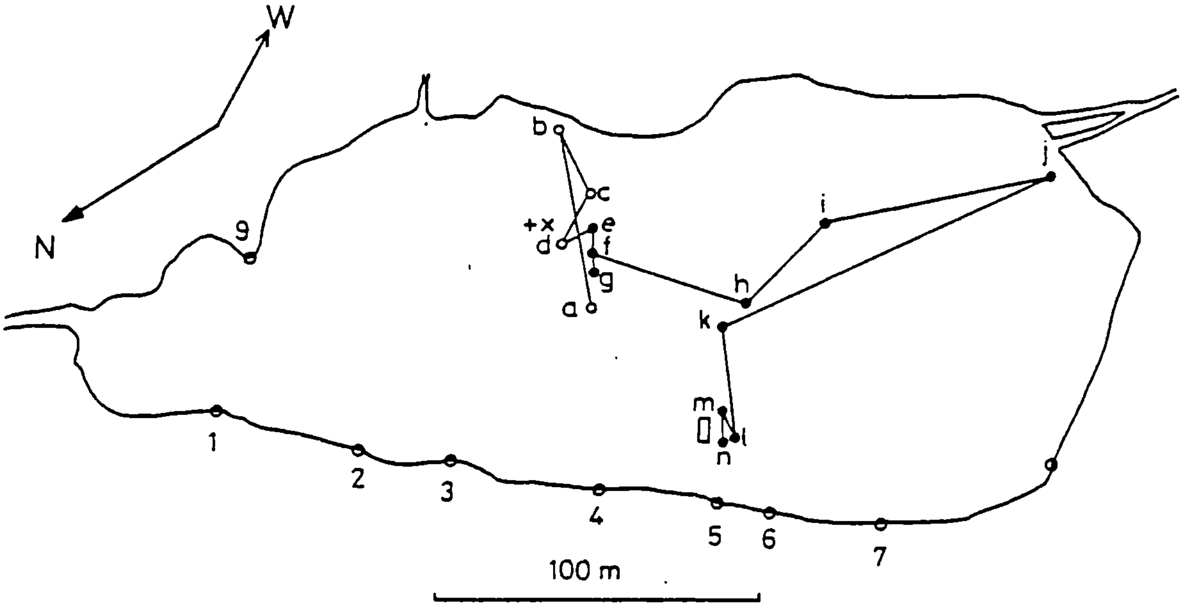
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Figure 3.25. The feeding behaviour of fish S2 on day 27 when there was no significant wind.

The fish was located, at the positions indicated, at the following times :

a. 1525, 1530

b. 1545

c. 1550, 1555

d. 1558

  1559 - conditioned stimulus on (+)

e. 1559, 1600

  1600 - conditioned stimulus on (+)

f. 1610

d. 1620

  1622 - conditioned stimulus on (+)

  1623 - food delivered (x)

  1626 - other fish start feeding at feeding station

g. 1705 - joins other actively feeding fish at the feeding station

h. 1712

  1718 - conditioned stimulus on (+)

  1719 - food delivered (x)

i. 1719

j. 1725

k. 1732 - located with actively feeding fish

l. 1740

m. 1744

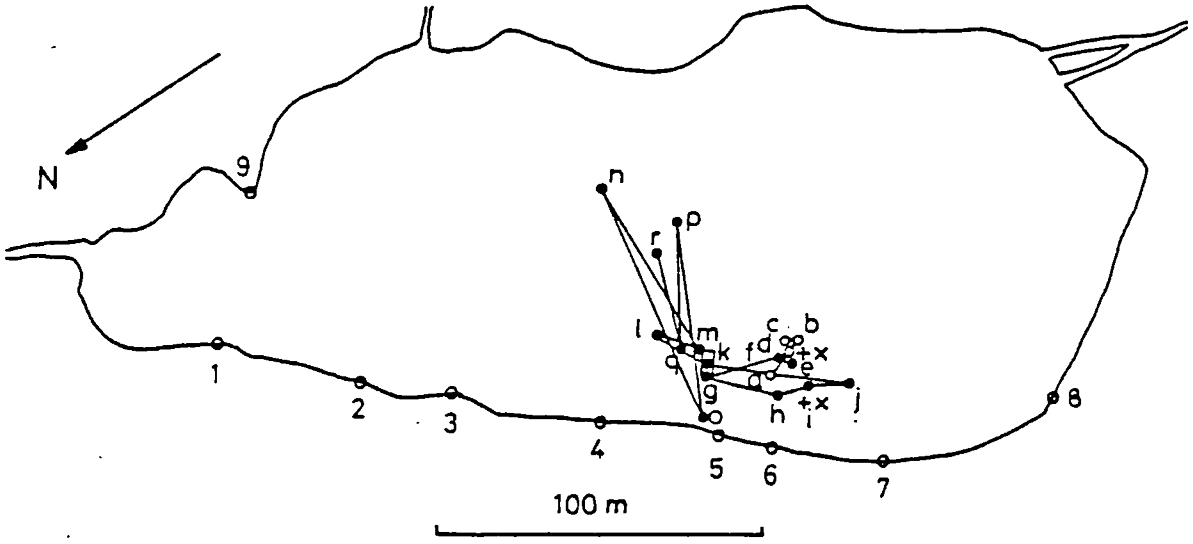
n. 1747

o. 1800

p. 1810

q. 1814

r. 1830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with other groups of feeding fish during feeding and this may have been because individual fish were attracted to common feeding points and/or because they were feeding in groups. Video observations supported the idea that at least some rainbow trout were moving around the loch in groups, because at non-feeding times small unpolarized groups (or shoals, Pitcher, 1979) were seen passing through the field of view.

3.3.2.7. The propagation of sound in Loch Charn

3.3.2.7.1. Introduction and methods

The aim of the work in this Section was to determine the distance over which the rainbow trout could have heard the conditioned stimulus.

Sound pressure, ambient noise and depth were measured from a boat moving along four transect lines radiating out from the feeding station (Figure 3.26,a). The loudspeaker was placed in its experimental position facing north-north-east at a depth of 3 m.

3.3.2.7.2. Results

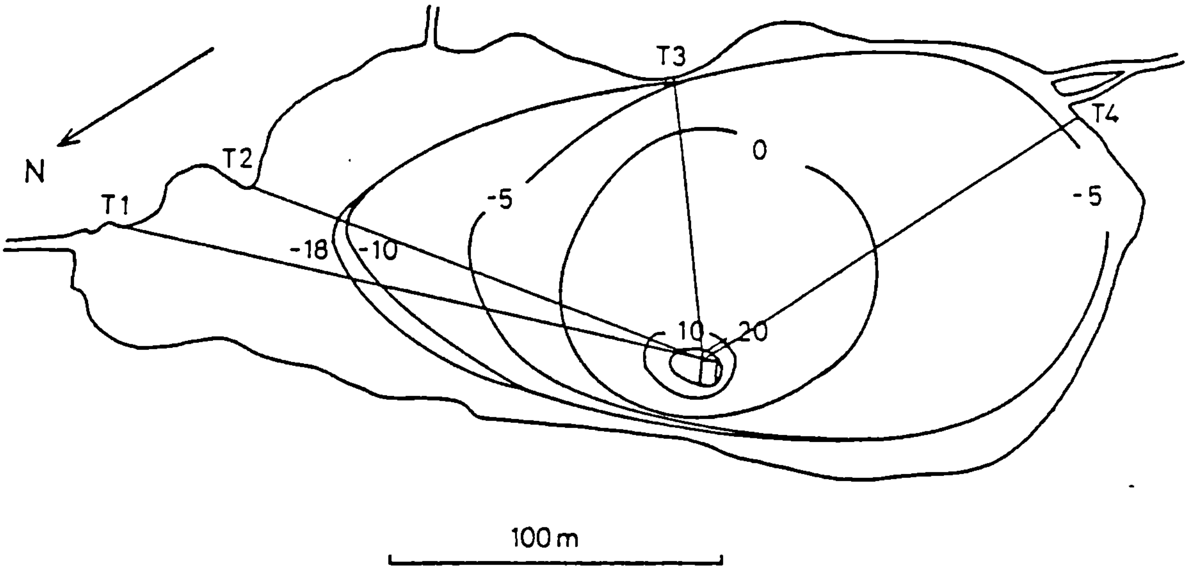
The sound signal was detected on the sound pressure level meter above background noise throughout the loch when the water was deeper than 2 m. At shallower depths the signal was rapidly attenuated to an undetectable level. For example, in transect 2 (Figure 3.26a) as the water depth decreased from 4 to 1.8 m there was a 12 dB drop to -20 dB// 1μbar within a horizontal distance of 5 m. Transect 3 was an exception to this rule with the signal being detectable at a level of -9 dB// 1μbar within 1 m of the bank with the hydrophone at 0.5 m and in 0.6 m of water. The reason for this difference was that transect 3 was over stony ground and the others were, in the shallows (< 5 m) at least, over muddy vegetated areas where signal propagation was severely limited.

To quantify the relationship between the sound pressure level and the distance from the sound source linear regressions were calculated of sound

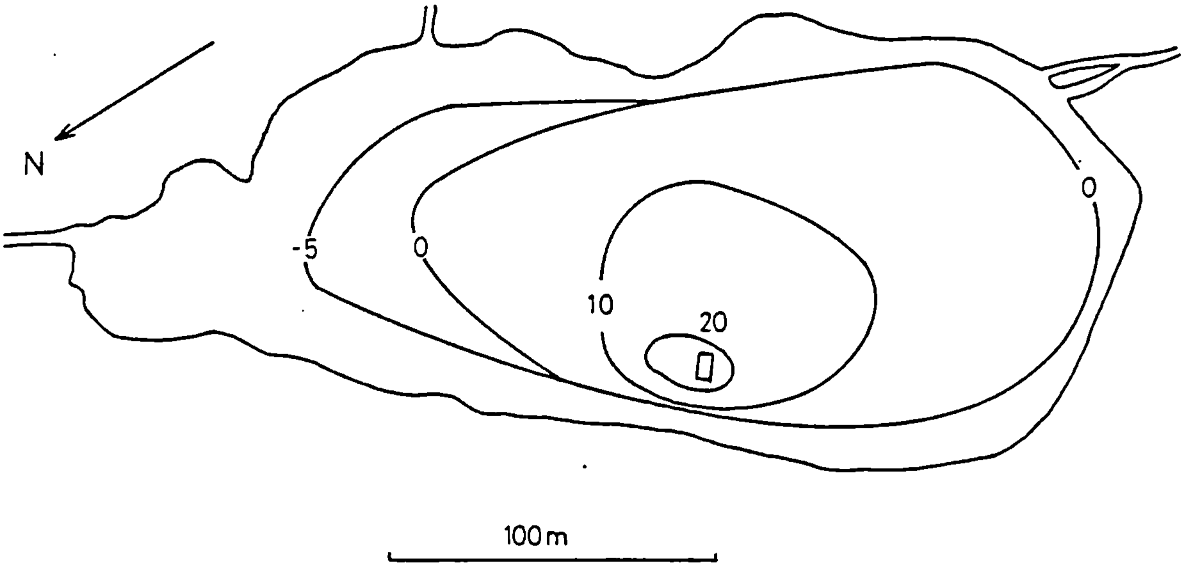
Figure 3.26. The propagation of sound in Loch Charn showing the transect lines (a) and sound pressure (dB // 1 µbar) contours throughout the loch for a receiver at a depth of 1 m (a) and 3 m (b). The outside contour on each map represents the position at which the signal was attenuated from the stated level of the contour to less than -18 dB // 1 µbar within a distance of less than 5 m.

i.e. the outside contour of -5 dB // 1µbar in (a) represents an approximate amalgamation of the contours of -5 dB, -10 dB and -18 dB // 1 µbar.

(a)



(b)



pressure (y axis) versus $\log_{10}$ distance (x axis) (Table 3.6). The regression coefficients of each transect line were then tested against the theoretical regression coefficients (β) assuming no loss with distance, spherical (β = -20) and cylindrical (β = -10) spreading from the source (Urick, 1975 and Section 2.3.3.). The results of these analyses (Table 3.6) showed that the observed propagation patterns could be explained in terms of both cylindrical and spherical spreading. Transect 1, with the receiver at 3 m depth was an exception to these rules as the attenuation was even greater than that expected with spherical spreading.

This variability between results was due to a variation in the depth of water and bottom type over which the transects were taken and a variation in the position of the receiver in relation to the loudspeaker. For example, the two transects T3 and T4, taken to the side and behind the loudspeaker respectively, were best described by the cylindrical spreading law as the sound propagated least well behind the transducer when the receiver was close to the source. Despite this variability in the data the regression equations of Table 3.6, together with the depth contours (Figure 3.1.), could be used to construct approximate sound pressure contours for the loch if one assumed that propagation was similar over similar depth contours in the same area.

Figure 3.26 illustrates how a sound pressure receiver at 3 m (Figure 3.26b) receives a higher amplitude signal over a greater range than one at 1 m (Figure 3.26a). It also illustrates how the signal propagated least well towards the shallower north-eastern end and propagated best over the deeper south western basin. As the signal reached shallower water it was severely attenuated with the result that in Figure 3.26 the outside contour may be taken as representing a short (< 5 m) transition between the stated contour and less than -18 dB// 1µbar.

The threshold for the conditioned response in Dunstaffnage Bay was 0 dB// 1µbar (Section 2). This result may perhaps be taken as a maximum

Table 3.6. A comparison of the experimental regression coefficients, for a receiver at 1 m and 3 m, with theoretical regression coefficients which assume no loss with distance ($\beta = 0$), cylindrical ($\beta = -10$) and spherical ($\beta = -20$) spreading. Distance (d) in m. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; rest, $p < 0.05$.

Transect	Depth of receiver (m)	d.f.	Regression equation; sound pressure =	t-value for -		
				$\beta = 0$	$\beta = -10$	$\beta = -20$
1	1	15	$41.88-25.80 \log_{10}d$	9.090***	5.568***	2.044
	3	14	$52.47-27.66 \log_{10}d$	12.167***	7.769***	3.371**
2	1	5	$35.58-21.45 \log_{10}d$	3.416*	4.002*	0.508
	3	5	$46.14-23.29 \log_{10}d$	14.105***	8.048***	1.991
3	1	9	$21.12-11.43 \log_{10}d$	2.385*	0.298	1.79
	3	9	$26.47-9.64 \log_{10}d$	2.716*	0.101	2.917*
4	1	12	$21.97-12.64 \log_{10}d$	2.602*	0.543	1.516
	3	11	$26.29-9.64 \log_{10}d$	2.892*	0.109	3.109**

threshold value above which the fish are certain to hear the signal. Hawkins and Johntone (1978), however, recorded minimum thresholds of Atlantic salmon to an 140 Hz signal of between -5 and 0 dB// 1μbar and even less under conditions of high particle motion which occur near the surface (Hawkins, 1973). Thus, the rainbow trout in Loch Charn may have heard the conditioned stimulus at levels below 0 dB// 1μbar although from the results of Section 2.3.2.5. this level should be used to estimate signal audibility. Using this level as the threshold one can predict that rainbow trout at 3 m would probably have heard the signal throughout the south western basin of the loch over water deeper than 4 m. For a rainbow trout at 1 m the range was more limited, although along T4 levels of greater than 0 dB// 1μbar were recorded at up to 120 m from the source. Therefore, depending on its position, a fish at 1 m could certainly have heard the signal at greater distances than that shown in Figure 3.26a. The attenuation into the north eastern shallows was much greater and thus beyond the contours the signal would certainly have been inaudible.

Ambient noise could conceivably have affected the range over which the signal was detectable. The measurements used for constructing Figure 3.26 were taken in a Force 2 wind at an equivalent sea state 1. The mean spectrum level of ambient noise taken at 1 m on this occasion was -42 dB// 1μbar/Hz (range 41.5 - 42.5; n = 3). Even if one assumes that the minimum audible 140 Hz signal is -5 dB// 1μbar the ambient noise must reach within 23.75 dB of this level (28.75 dB// 1μbar/Hz) before any masking occurs (Hawkins and Johnstone, 1978). This level of ambient noise is + 13 dB greater than wind Force 2, sea state 1, conditions in Loch Charn and greater than the levels recorded by Hawkins and Johnstone (1978) in a fast flowing river (-33 dB// 1μbar/Hz) or under Force 4 (sea state 3) conditions in the sea (-34 dB// 1μbar/Hz). In Dunstaffnage Bay a spectrum level of -30.5 dB// 1μbar/Hz was recorded at sea state 3. In rougher conditions the ambient noise in the loch may have been greater than the sea as a result of wave action on the shores, although the size and sheltered position precluded a large surf developing. The maximum wave height observed in a Force 7 wind was approximately 0.5 m, which only corresponds to sea state 3 (Wenz, 1962), and therefore ambient noise was unlikely to have reached a level at which there was masking of a -5 dB// 1μbar signal. Thus, ambient noise probably had little affect (except perhaps very close to the surface) on the range over which the conditioned stimulus was heard.

3.3.3. A summary of the work in Loch Charn

From the results of Sections 3.3.1. and 3.3.2. it was apparent that in both the short and the long term rainbow trout could be attracted from anywhere in this small loch to feed at the feeding station without a sound stimulus. There appeared to be no advantage to pre-conditioning fish prior to release although it may be predicted from the results of Section 2 that as fish tended to aggregate around the feeding station then they could easily be conditioned in situ. Conditioning may therefore still be a useful technique for a more precise control of rainbow trout movements and although it appears to be unnecessary for feeding it may perhaps be more purposefully used for harvesting the stock. The adverse conditions described in Section 3.3.2., in particular the presence of a predator and the windy weather, precluded such conditioning and the development of the experiments in this direction.

3.3.4. Returns, growth and diet of stocked fish

3.3.4.1. Return of stocked fish

Of the 188 rainbow trout released into the loch on 23 April 1980, 104 tagged fish were returned by anglers by 22 September 1980 (day 152). There were also three untagged rainbow trout captured during this period and, although these fish were not examined for tag scars, because there was no evidence of any rainbow trout in the loch before stocking, these fish were probably rainbow trout originating from the present stock but which had lost their tags. This represents a tag loss of 1.8%/100 days (2.8% in total) which compares well with that reported for brown trout by Thorpe (1974 b) (1.2%/100 days) and Templeton (1971) (11.8% -21.3%/100 days) and Atlantic salmon smolts by Ritter (1973) (in Eisner and Ritter, 1979) (11.0%/30 days). The return may therefore be corrected to 107 fish which represents a 56.9% return on stocking. Only 22 out of 35 of the angling return forms were recovered over this period, however, because some anglers removed but did not return them. The mean number of fish recorded on the recovered forms was 2.95 (s.d. = 2.24; n = 22) and if it is assumed that the unreturned forms contained the same number of fish as the returned forms then the return on stocking may be corrected to a total return of 77.3%. This assumption may not be correct as Coles (1981) found that anglers who did not return forms usually caught less than those who completed them. This bias will, however, be balanced, to an unknown degree, by the anglers who caught fish but did not even remove a form (observed on one occasion). Similarly, Thorpe (1974b) and Moring (1980) found that anglers reported only between 43% and 71% of the tagged fish that they captured.

The return for the September stocking was 18.0% (31 fish). Of these, six fish were caught during April 1981 which represents an overwintering survival of 4.1%.

3.3.4.2. Temporal pattern of angling returns

There was an initial peak in the number of tagged rainbow trout captured outside the feeding area within the first 21 days after the April stocking (Figure 3. 27). After this period there was a decline in the recorded catches and, although no quantitative description of angling pressure was obtained, this

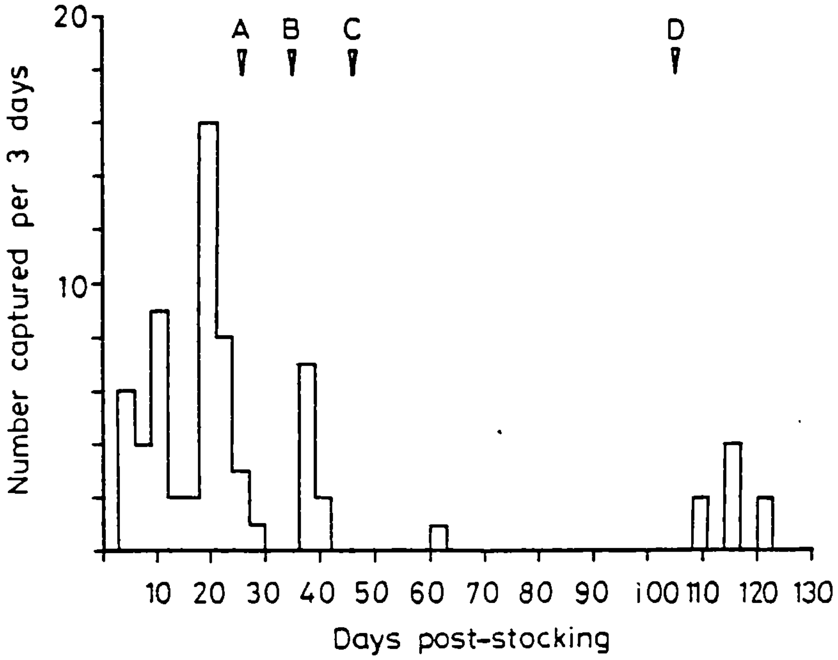


Figure 3.27. The number of fish captured by anglers outside the feeding area as indicated by the return of completed angling returns. Arrows represent the days on which the size of the feeding area was increased (A), the ration was reduced to the 10% level (B), increased to 100% again (C) and the time at which supplementary feeding was stopped (D).

reduction probably reflects more of an increase in the percentage of the stock that were aggregating at the feeding station rather than a variation in the number of anglers fishing, although angling pressure may have been reduced when anglers were less successful. There was a small increase in the number captured outside the feeding area after the ration level was decreased and after feeding was stopped (Figure 3.27) which shows that a decrease in the feeding level stimulated fish to move away from the feeding station.

3.3.4.3. Spatial pattern of angling returns

In both experiments fish were captured throughout the loch after stocking. These fish were captured 6 and 5 days after stocking in April and September respectively suggesting that after this period of time they had distributed themselves throughout the loch (Figure 3.28). This finding confirms those of the ultrasonic tagging experiments.

Fish with pellet remains in their stomachs were also captured throughout the loch suggesting that some fish were making excursions away from the feeder after feeding. In particular, one individual was captured at the north-north-eastern end of the loch, approximately 150 m from the feeder, with whole pellets in its stomach at 1700 and, as pellets were confined to the feeding area on this occasion, this fish had certainly fed at the feeder within the previous hour (feeding time 1600). Grove et al. (1978), in a laboratory study, showed that a 300 g rainbow trout takes 59 and 44 h to empty its stomach at 8.5°C and 14°C respectively after a 1% body weight meal of trout pellets. Therefore, in spite of the fact that evacuation times may show considerable individual variation (Windell et al. 1976), and fish may evacuate their stomachs quicker in the field (Thorpe, 1977), these times suggest that, for the April stocking at least, fish with traces of pellets in their stomachs had probably fed at the feeder within the previous 2 or 3 days. In September, because the pellets were

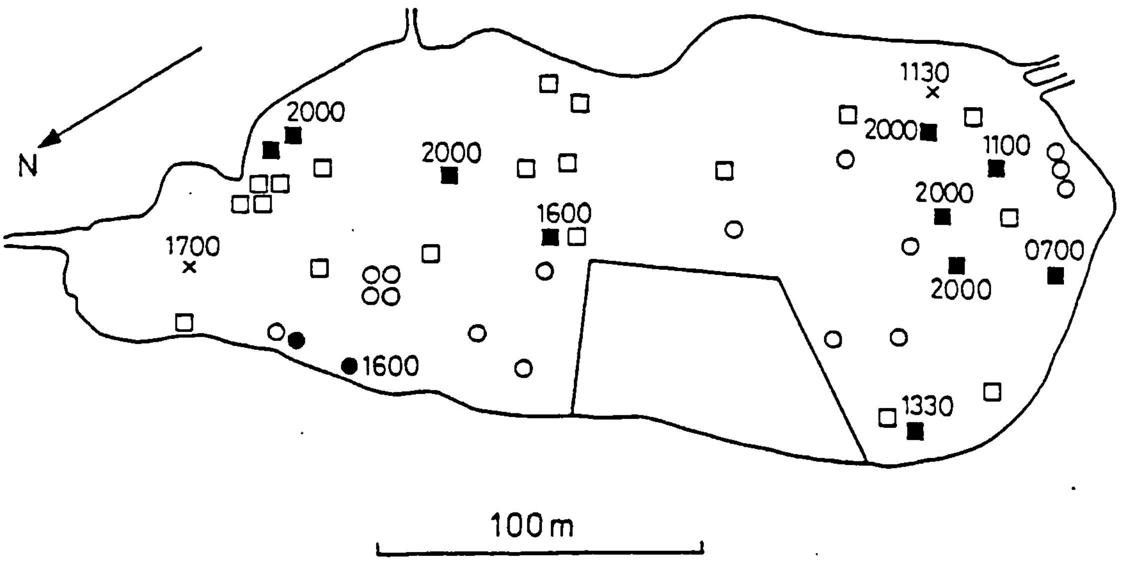


Figure 3.28. Approximate position of the fish caught by anglers.
April stocking : 0-30 days post release with (■) and without (□) pellets in their stomachs; 30 + days with (●) and without pellets (o).
September stocking : 0-10 days with pellets in their stomachs (X) (fish captured by anglers using artificial food as bait are excluded)
The time (BST) at which fish with pellets in their stomachs were caught is also indicated.

not always confined to the feeding area, fish with pellet remains in their stomachs may not have fed at the feeder.

3.3.4.4. Growth rate of stocked fish

The specific growth rates (s.g.r.s.) of fish in Loch Charn are given in Table 3.7. Some negative s.g.r.s, which are theoretically impossible, were obtained and these may have been a result of shrinkage (Templeton, 1971) or an error in measurement. They were, however, included in the calculation of the mean as all measurements may be subjected to the same error.

Supplementary feeding was stopped 110 days after their introduction into freshwater in April and there was a significant negative correlation between the s.g.r. of fish caught after this date and the time after which feeding was stopped (tau = -0.502; n = 38; $p < 0.001$). As fish were caught both inside and outside the feeding area angling was probably a random process with respect to the stock. This result suggests that supplementary food was therefore essential to maintain the growth rate that had been maintained since April.

After the April stocking the mean s.g.r. for the first 67 days (Table 3.7) was significantly lower than that for the period between 110 and 157 days (t = 3.870; d.f. = 72; $p < 0.001$). There was also a significant decrease in the coefficient of variation (Sokal and Rohlf, 1969; Lehner, 1979) between the two samples (days 17 - 67; CV = 53.13%; days 110 - 157; CV = 20.28%; test statistic, C = 4.007; d.f. = 72; $p < 0.001$). This difference in variation probably reflects both errors in the measurement of the smaller length increments and a variation in the feeding opportunity during the earlier period.

Similarly, there was a large coefficient of variation (CV = 54.31%) about the mean s.g.r. for the rainbow trout stocked in September (Table 3.7). This mean was not significantly different from that of the initial sampling period after the April stocking (t = 0.872; d.f. = 57; $p > 0.1$) even though the temperature was higher during September.

Table 3.7. Specific growth rate (s.g.r.) of stocked fish (% of body length/day)

* time since introduction into freshwater.

Stock	Time of capture * (days)	n	Mean s.g.r. (± 1.s.d.)
April	17-67	36	0.2174 (±.1155)
April	110-157	38	0.2998 (±.0608)
Sept	10-14	23	0.2460 (±.1336)

Table 3.8. The effect of stomach content on the specific growth rate (% of body length/day)

* time since introduction into freshwater.

Stock and capture time	Food in stomach	n	Mean	(± l.s.d.)	t value & significance
April days 17-35*	Pellets	14	0.1998	(± 0.0739)	t = 0.402 d.f. = 20 $p > 0.1$
	No pellets	8	0.1855	(± 0.0910)	
Sept. day 10*	Pellets	7	0.2377	(± 0.1165)	t = 0.461 d.f. = 8 $p > 0.1$
	No pellets	3	0.2717	(± 0.0705)	

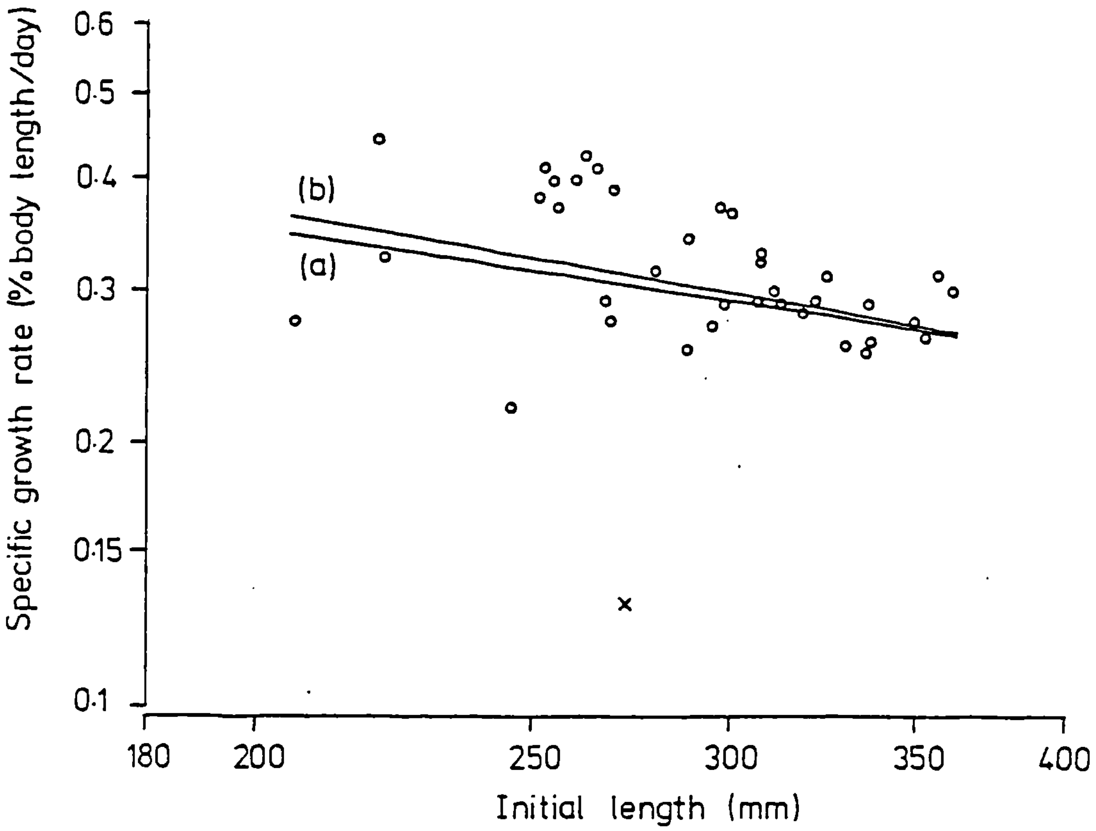


Figure 3.29. The relationship between the natural logs of the specific growth rate and stocking length of the rainbow trout captured in Loch Charn more than 105 days after stocking. Regression line (a) includes all points and is not significant ($p > 0.05$). Regression line (b) excludes the anomalously low point (X) and is significant ($p < 0.01$).

If variations in the amount of feeding contributed to the variability in growth rate then fish with pellets in their stomachs might have been expected to show higher growth rates than other individuals. There was no such evidence (Table 3.8) suggesting that, at least for fish outside the "forbidden" feeding area, there was no variation in the opportunity to feed at the feeding station. This result concurs with the findings of the ultrasonic tagging experiments because there should have been no differences in the growth rate if all fish were capable of being attracted to the feeding station.

3.3.4.5. The relationship between stocking length and subsequent growth rate

Preliminary analysis suggested that there was no significant relationship between s.g.r. and the length of the fish at stocking (Figure 3.29). There was, however, an anomalously low s.g.r. for a fish of 273 mm (point marked) and, using a technique of Snedecor and Cochran (1978), the deviation of this point was shown to be significantly different ($p < 0.05$) from the line that was calculated without using this point (Figure 3.29). This fish was in fact a small mature male which are commonly found to have low s.g.r.s and, as such, is an aberant point which may be validly omitted from the calculations (Snedecor and Cochran, 1978). When the regression was recalculated without using this point, it was significant showing that there was a negative linear relationship between the natural logarithm of the s.g.r. and the natural logarithm of the length (Figure 3.29).

There were no other significant relationships between stocking size or condition factor and survival or growth rate.

3.3.4.6. Composition of the diet

Table 3.9 summarizes the composition of the diet of all the rainbow trout captured in Loch Charn and a more detailed presentation of the natural animal

Table 3.9. The relative importance of the three main dietary components of the rainbow trout in L. Charn during the three sampling periods. Artificial food was used as bait to capture fish during periods 2 and 3(b). (* all except one captured between days 105 and 127). Further details of the animal component are given in Appendix B.1.

Stocking month and post-stocking sampling period	n	Food Item	Occurrence (% occurrence)		Dry weight index (% total dry weight index)	
April		Artificial	8	(44.44)	14.81	(45.02)
days 12-39	18	Plant	11	(61.11)	14.19	(43.13)
(1)		Animal	12	(66.67)	3.90	(11.85)
		Empty	2	(0.11)		
April		Artificial	31	(91.18)	100.6	(92.35)
days 105-152*	34	Plant	11	(32.35)	1.86	(1.71)
(2)		Animal	27	(79.41)	6.47	(5.94)
		Empty	0	(0)		
Sept.		Artificial	4	(57.14)	15.48	(81.47)
day 6	7	Plant	1	(14.29)	0.48	(2.53)
(3a)		Animal	5	(71.43)	3.04	(16.0)
		Empty	0	(0)		
Sept.		Artificial	5	(100.0)	13.90	(77.39)
day 10	5	Plant	2		1.48	(8.24)
(3b)		Animal	4	(80.0)	2.58	(14.36)
		Empty	0	(0)		

component of the diet is given in Appendix B.1.

A comparison of the results of the occurrence and dry weight methods in Table 3.9 shows that the occurrence method overestimates the importance of natural food and that the dominant component of the diet on all the different sampling occasions is artificial food. There is, however, a strong bias in these results as a result of using artificial food for bait during sampling periods 2 and 3b (Table 3.9). These variations between individual periods are considered separately in the following section.

Plant material was collected at all times (40.62% total occurrence) and contributed a large proportion to the dry weight of the contents of some stomachs. The majority of this item would have been taken from the surface and may have been ingested deliberately or accidentally, perhaps whilst foraging for floating insects amongst detritus which would also have collected in similar places.

Of the animal component of the diet there was an obvious preference for surface food. Mollusca, chironomid larvae and a plecopteran nymph were the only members of the bottom fauna (includes fauna on vegetation) eaten and represented only 6.04% of the total numbers of animals consumed. Ephemeropteran nymphs are associated with the bottom or vegetation but only nymphal skins were found in the stomachs and these would have been taken from the surface after emergence of the sub-imago. Cladocera (water fleas) and Acarina (water mites) would have been taken from mid-water and chironomid pupae, which were the single most abundant item in terms of numbers, would have been taken as they were rising to or at the surface. All adult insects would have been taken from the surface and represented 57.49% of the total number of individuals consumed. There was a very significant terrestrial input as 37.92% of the total number of animals consumed are known to have terrestrial larval stages. Some of these, such as Geotrupes stercocarius

(Coleoptera), Apis mellifera (Hymenoptera) and Pentatoma rufipes (Hemiptera), are large insects which represent a high net energy gain per unit effort. Ants, particularly Myrmica scabrinodis, were abundant in some stomachs.

3.3.4.7. Temporal variations in the diet

There was a significant increase ($\chi^2 = 11.33$; d.f. = 1; $p < 0.001$) in the frequency of occurrence of pellet remains between sampling periods 1 and 2, primarily because fish were captured using pellets as bait during the latter period. However, when fish were aggregated close to the feeding station they would probably also have contained a large proportion of pellets and, as such, period 2 when 31 fish were captured in the feeding area, was probably analogous to this situation. During periods 1 and 3a (Table 3.9) only 44% and 57% of the stomachs respectively contained pellets and this result shows that during the development of the response to the feeding station, although fish may potentially have been attracted from anywhere in the loch to feed, they were not all attracted at once.

Although examination of Table 3.9 suggests that during period 1 fish were consuming a higher proportion of plant material and, indeed, there was also a greater mean dry weight of plant material per stomach during this period (period 1; mean 0.167 g; range 0 - 1.056 g: period 2; mean 0.023 g; range 0 - 0.451 g: period 3; mean 0.025 g; range 0 - 0.251 g), there was no significant difference in the frequency of occurrence (χ^2 test; $p > 0.05$) or dry weight of material per stomach (Mann-Whitney U test; $p > 0.05$) between any of these sampling periods.

There was a significant increase ($\chi^2 = 5.78$; d.f. = 1; $0.02 < p < 0.05$) in the frequency of occurrence of Hymenoptera between sampling periods 1 and 2. This increase was primarily due to an increase in the number of ants, both winged and apterous, consumed. There was no significant change ($p > 0.05$) in the relative occurrence of any other animal items during this study period.

During periods 1 and 3a, when fish were captured throughout the loch, natural animal food comprised 12% and 16% respectively of the diet as judged by analysis of the dry weight index. When fish were aggregated, and hence more limited in their movements, they may have had less opportunity to feed on natural food even though, by having fed in the loch for a while, they would have increased their potential natural dietary input through experience (Sosiak et al., 1979). Even so, on day 105, the day on which feeding was stopped, which may perhaps be taken as representative of an aggregated condition, there was no significant difference in the frequency of occurrence (χ^2; $p > 0.05$) or dry weight of natural food items per stomach (Mann-Whitney U test; $p > 0.05$) when compared with period 1. After this date, however, there was a significant positive correlation (tau = 0.465; n = 34; $p < 0.001$) between time and the dry weight of animal food per stomach suggesting that whilst fish were at the feeding station they may not have been making optimal use of natural food. Stopping or perhaps limiting supplementary feeding could therefore improve the utilisation of this resource.

3.3.5. Brown trout

3.3.5.1. Diet and growth

Details of the captured brown trout are shown in Table 3.10. No brown trout caught outside of the feeding area contained any trace (in either stomach or intestine) of artificial food suggesting that these fish were not feeding at the feeder. One fish was captured in the north-north-eastern bay using a pellet as bait suggesting that some brown trout would have fed on artificial food if they were given the opportunity. This suggestion was confirmed when three fish were captured on artificial food inside the feeding area, showing that at least some brown trout were feeding on pellets near the feeding station.

No detailed analysis was made of the natural food consumed because of the small sample size obtained and therefore no comparison can be made

Table 3.10. Details of the brown trout captured in Loch Charn.

Date of capture	Fork length (mm)	Age	Notes on position of capture and stomach contents
18 May 1978	125	2+	Captured outside the feeding area. Feeding on natural food although the feeder was operational at this time.
	180	3+	
	173	3+	
	205	3+	
14 May 1980	193	-	Captured outside the feeding area. Feeding on natural food.
15 May 1980	224	-	
18 May 1980	170	-	
12 August 1980	212	3+	Captured next to feeder. Natural and artificial food in stomach.
19 August 1980	-	-	2 fish captured in feeding area using pellets as bait. The stomach contents were not available for inspection.
22 September 1980	175	3+	Empty stomach although captured using a pellet as bait at the northern end of the loch.

between the feeding habits of brown and rainbow trout. Qualitative analysis of data from a previous study in Loch Charn in 1978 (R. Gibson, pers. comm.) and the present study (both combined in Table 3.11) suggests that surface insects again comprised a major component of the diet. The occurrence of a large number (120) of Daphnia pulex in one stomach and of trichopteran larvae, which were not found in any rainbow trout stomachs, suggests that there may be some differences in diet which may perhaps be explained by some size dependent selection (for Daphnia) and a greater propensity for mid-water and bottom feeding.

The age and fork length of the brown trout gives some indication of their growth rate which may be compared with the data given by Campbell (1971) of the growth of brown trout in a variety of Scottish freshwater lochs. The Loch Charn population falls into his category of 'small slow growing fish' which is indicative of the limitations of available natural food for the size of population. Fish which learnt to consume artificial food would therefore have been expected to show a subsequent improvement in growth rate.

3.3.5.2. Video observations

From 30 July 1980 until 4 August 1980 the television camera was attached to the surface structure of the feeding station at a depth of 15 cm and at an angle of 45° to the horizontal and video recordings of fish behaviour were taken around the feeding times for both 1.5 min before and 1.5 min after feeding.

The majority of fish seen were rainbow trout which could be identified by their body markings and the yellow tag and tag scars below the dorsal fin. Smaller, darker, unscarred fish were also seen feeding and these were thought to be brown trout. A maximum of three of these fish were seen in the field of view at any one time and,because they were often observed within 5 s of a food delivery, this suggests that they were part of the population that were

Table 3.11. Stomach contents of brown trout expressed in terms of their percent occurrence. Eight stomachs examined.

Item	Occurrence	
	n	%
Class Insecta larvae (inc. chironomid larvae and Trichoptera larvae)	4	50
Class Insecta adults (Diptera, Hemiptera and Hymenoptera (ants))	6	75
Daphnia pulex	1	12.5
Gastropoda	2	25
Plant Material	2	25
Artificial food	1	12.5
Empty	1	12.5

aggregated at the feeding station at this time. When the camera was placed in its normal position below the feeder up to a maximum of three obviously smaller fish, which were probably brown trout, were counted amongst a group of 39 fish. Apparently, then, a small number of brown trout had learnt to feed and become part of the group of fish close to the feeding station.

3.3.6. Experiments in Loch Fad

3.3.6.1. Introduction

Two possible lines of research could have been followed after the Loch Charn experiments. One was to continue these experiments as outlined in 3.3.3., condition fish in situ, and evaluate the limitations and usefulness of sound for controlling the movements of fish in and around the loch. The second approach was to examine the attraction to and aggregation around supplementary feeding points in a much larger body of water to see whether the findings from Loch Charn were generally applicable to larger lochs. An opportunity arose to take the latter approach at Loch Fad, a larger eutrophic lowland type loch on the Isle of Bute. This loch not only provided a contrast to Loch Charn in terms of size but also in terms of its productivity and therefore the availability of natural food.

Supplementary food is introduced into Loch Fad accidentally as waste from the cages of a rainbow trout farm. Both artificial food and trash fish are fed to the caged fish and an unknown proportion of this food becomes available to the free-swimming rainbow trout which inhabit the loch. The work presented here is an attempt to examine the movements of these rainbow trout in relation to these supplementary feeding points.

3.3.6.2. Materials and methods

3.3.6.2.1. Experimental site

Loch Fad (Figure 3.30) is a shallow eutrophic lowland type loch (Latitude 55° 48' - 55° 49' N, Longitude 5° 04' W) approximately 2.5 km long and 0.3 km wide with a maximum depth of 12 m. There is one main and five minor feeder streams and the level is regulated by a sluice at the only outflow at the north-eastern end. A more detailed description of, and the effect the fish farm has had on, the loch is given by Beveridge (1981). The rainbow trout farm comprises six sets of cages in the northern basin of the loch (Figure 3.30) and food is potentially available from all of them.

The rainbow trout examined during this study were all escapees from the cages. In addition, pike, Esox lucius, eels, Anguilla anguilla, perch, Perca fluviatilis, and roach, Rutilus rutilus also inhabit in the loch.

Angling is allowed in the loch and is carried out from the shore and boats with no restriction placed on the method. No angling is allowed around the cages so that fish aggregating in this area are potentially unavailable to any anglers fishing the loch.

3.3.6.2.2. Mark/recapture tagging experiments

Fish were captured for tagging with a 37 m long beach seine, 1.8 m deep and with a mesh size of 9.5 mm in the bunt. The net was set roughly parallel to, and approximately 40 m out from, the shore. It was then retrieved by pulling on the ropes attached to either end so that it swept an area of approximately 1480 m^2. Sampling was carried out during daylight hours at the sites marked in Figure 3.30.

Fish were also captured from outside Cages IV and VI (Figure 3.30). The corners of a 6 m x 4 m x 4 m cuboid shaped bag net were weighted and the open top lowered approximately 3 m below the surface. Small amounts of artificial trout food and trash fish were then fed in the centre of the cage for periods of

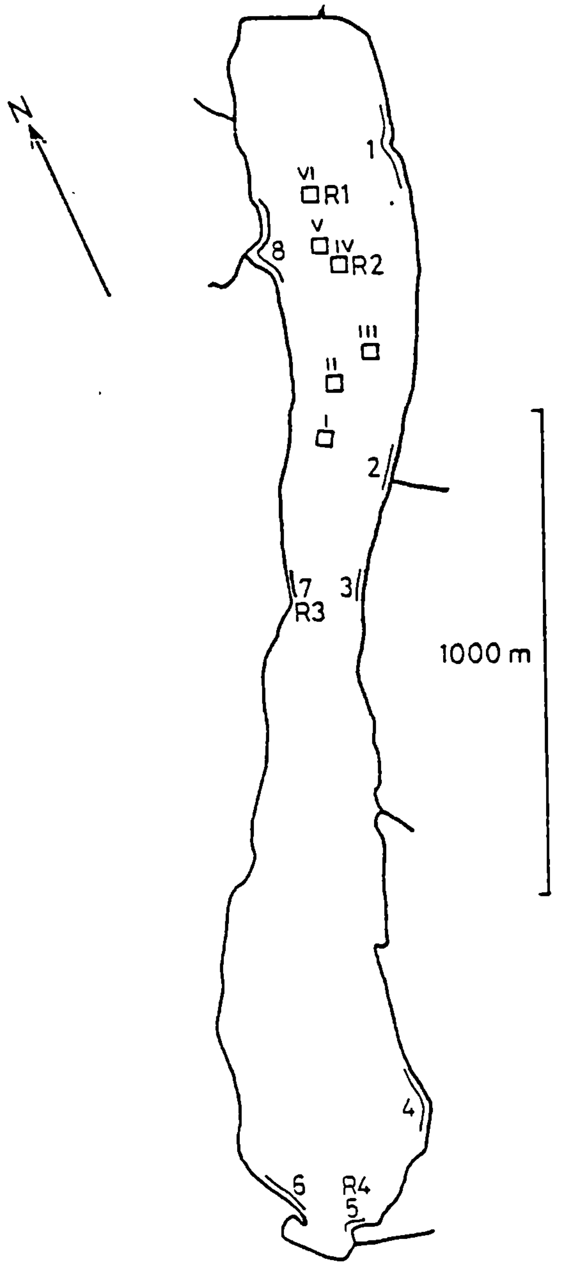


Figure 3.30. Loch Fad (Latitude 55°48' - 55°49'N, Longitude 05°04'W) showing the approximate position and numbering of the fish cages on 2 May 1981. Beach seining sites (numbered 1-8) and release sites R1-R4 are also shown.

up to 30 min. The net was then quickly raised and fish that were attracted to the food were caught in the net.

Fish were tagged using the same tag and tagging technique described in Section 3.2.2. and were all individually weighed (nearest 5 g) and measured (fork length; nearest mm) prior to release. Fish were allowed to recover from the anaesthesia, occasionally overnight in the nets on the trout farm, prior to release.

Three separate types of experiments were carried out with two different stocks of fish. The following descriptions are used for these fish:

1. Stocked fish: fish originally in the cages but released into the loch at the start of the experiments.
2. Naturalized fish: fish captured in the loch both outside and close to the cages and from the shore.

Sampling was carried out on three separate occasions (Table 3.12).

Fish were recaptured by netting from the cages, beach seining, gill netting once, and by anglers. A bailiff was employed at the water and was requested to weigh, measure and record the tag numbers and capture position of all the tagged rainbow trout that were recaptured in the author's absence.

In addition to the above, the stomach contents of fish captured from the shore and the cages were examined on the three sampling occasions. The oesophagus, stomach and intestine were removed from the fish and preserved in 70% alcohol. Contents from the stomach and oesophagus were pooled and analysed according to the methods of Section 3.2.5. The intestine was examined separately.

Table 3.12. Details of the stocks of rainbow trout tagged in Loch Fad. Release points refer to the beach seining sites and cages shown in Figure 3.30.

STOCK	NUMBER OF FISH	DATE OF RELEASE	CAPTURE POINT	RELEASE POINT	NOTES
Stocked Fish	64	28 April 1981	All initially from cage stock (Cage IV and VI)	Cage VI	
	38	29 April 1981	"	Cage IV	T = 9°C
	39	28 April 1981	"	Site 7	
	31	28 April 1981	"	Site 5	
Naturalized Fish	7	28 April 1981	Captured around and held in Cage VI for up to 10 days prior to release	Cage VI	T = 9°C
	10	27 April 1981		Site 5	
Naturalized Fish	98	27 April 1981 to 2 May 1981	Captured by beach seine and released in the same position		T = 9°C
Naturalized Fish	71	3 June 1981 to 5 June 1981	Captured by beach seine and released in the same position		+ 5 captured but untagged
	99	4 June 1981 to 5 June 1981	Captured and released at Cage VI		T = 15°C + 10 captured but untagged
Naturalized Fish	86	30 July 1981	Captured and released in same position		T = 17°C
	36	30 July 1981	Captured and released at Cage IV		None tagged. Weighed and measured only

3.3.6.2.3. Ultrasonic tagging

Ultrasonic tagging work was carried out in association with Dr L. Ross and Dr M. Beveridge of the University of Stirling. The experiments were carried out from 28 April 1981 until 3 May 1981. Two rainbow trout were captured for tagging by angling from the cages and the other fish came from the farm stock within the cages. The tags and tracking equipment used were identical to those described in Section 3.2.7. Tagged fish were located either by triangulation from the shore or from a boat by moving the boat close to the fish, estimating the range, and then fixing the position of the boat with reference to known shore locations. The latter method is described in more detail by Thorpe et al. (1981). There was considerable daily boat activity in the loch so it was unlikely that these methods seriously disturbed the fish.

3.3.6.3. Results

3.3.6.3.1. The movements of tagged fish in Loch Fad

Sixty three tags were returned by 6 August 1981, which, if one excludes the second return from a fish that was caught twice, represents a 13.57% return of the 457 fish tagged. Table 3.13 gives a breakdown of the returns. Fish were recaptured by angling (58.73%), beach seining (19.05%), netting from the cages (20.63%), and gill netting (1.59%). Those fish that were captured in the beach seine or by the author by netting at the cages were weighed, measured and released immediately.

For further analysis the loch was divided into a northern and southern basin by an imaginary dividing line running across the loch immediately south of beach seining sites 7 and 3 (Figure 3.30). Fisher's exact probability test (Siegel, 1956) was then used to test the null hypotheses that there was no significant difference in the proportion of tag returns from each stock (e.g. naturalized and stocked or naturalized southern basin and naturalized northern basin) in any

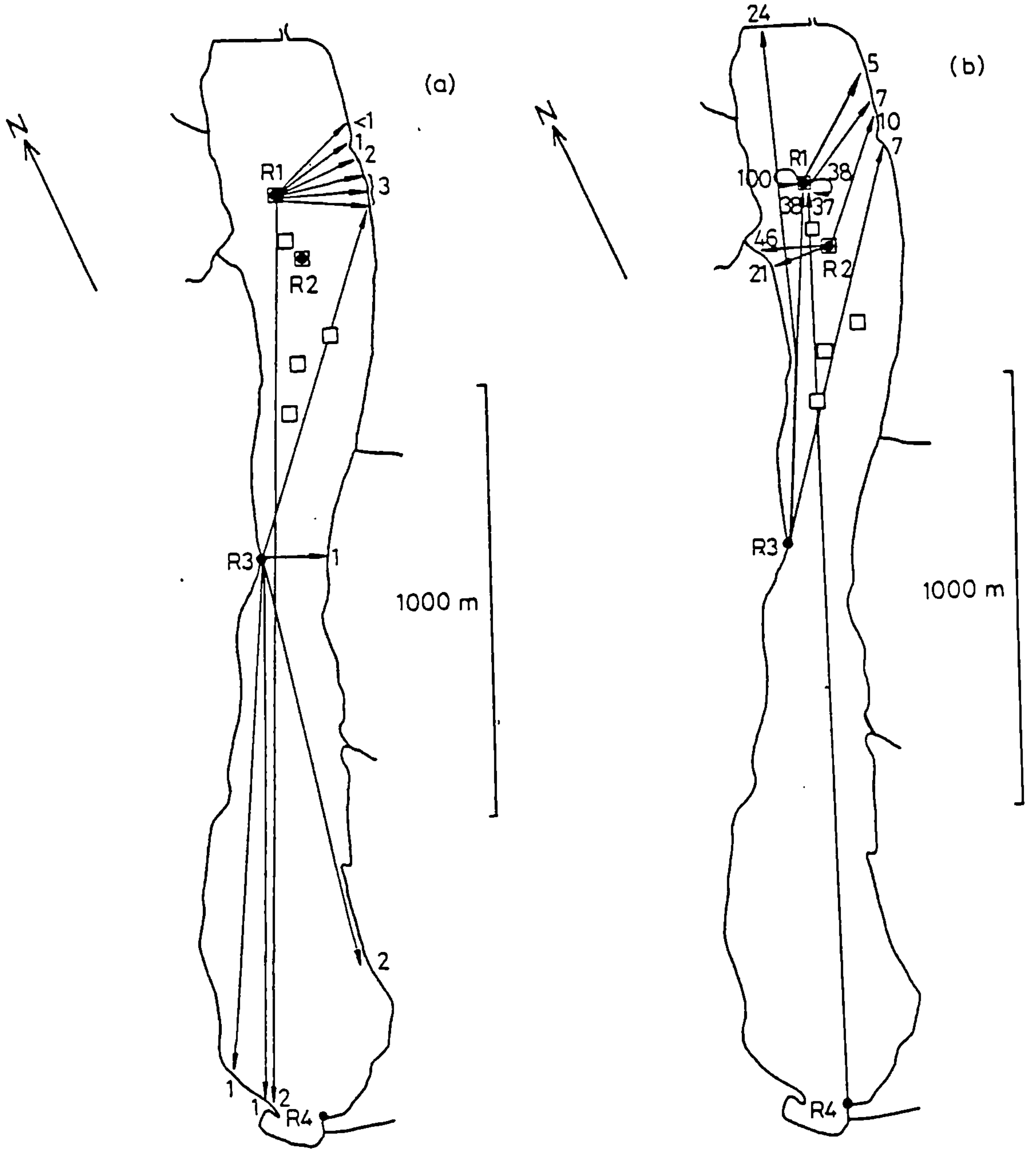
Table 3.13. A summary of the returns of naturalized (N) and stocked (S) rainbow trout in Loch Fad, showing release points and recapture areas. (One naturalized fish captured, tagged and released in the southern basin was recaptured but no details were given by the angler and it is therefore excluded from the table). (* indicates where a fish was caught that had been recaptured previously). Numbers in brackets indicate the number of fish of a given stock captured by anglers within 30 days of tagging which were used in the text for χ^2 analysis.

	Release/tagging position							
	N. basin (littoral) (N)	S. basin (littoral) (N)	N. basin (Cage VI) (N)	N. basin (Cage VI) Displaced to Site 5 (N)	N. basin (Cage VI) (R1) (S)	N. basin (Cage IV) (R2) (S)	Site 7 (R3) (S)	S. basin (Site 5) (R4) (S)
Number released	102	67	106	10	64	38	39	31
Number captured in N. Basin (littoral)	11 (7)	1(1) (+ 1 in gillnet 50 m east of Cage IV)	2 (1)	2	8 (6)	3	4	-
Number captured in N. basin (Cage VI) (** Cage II)	4	2	8	1*, 1**	2	-	1	1
Number captured in S. basin (littoral + boat)	1	3	1	1	1	-	3	-

Figure 3.31. The movements of stocked rainbow trout (originally from caged stock) released at R1 - R4. The time (days) between their release at ● and subsequent recapture is shown adjacent to their recapture point.

(a) shows the movements of fish recaptured within 3 days of being released.

(b) shows the movements of fish recaptured greater than 3 days after being released.


(a)
N
<1
1
2
3
R1
R2
R3
1
1000 m
2
1
1
1
2
R4
(b)
N
24
5
7
10
7
R1
100
38
38
37
46
21
R2
R3
1000 m
R4

particular population (e.g. angler or cage captured) of tag returns. Where the data from angler caught fish is considered it refers only to those fish caught within 30 days of tagging. A 30-day period was chosen to enable returns from fish stocked at different times to be compared.

3.3.6.3.2. The movements of stocked fish

The fact that tagged, stocked fish were recaptured throughout the loch within 48 h of being released (Figure 3.31a) suggests that, like Loch Charn, fish spread rapidly throughout the loch after stocking. This view was reinforced by some untagged fish, recognisable by their ragged fins and poor condition, that were caught in the beach seine within 24 h of being released.

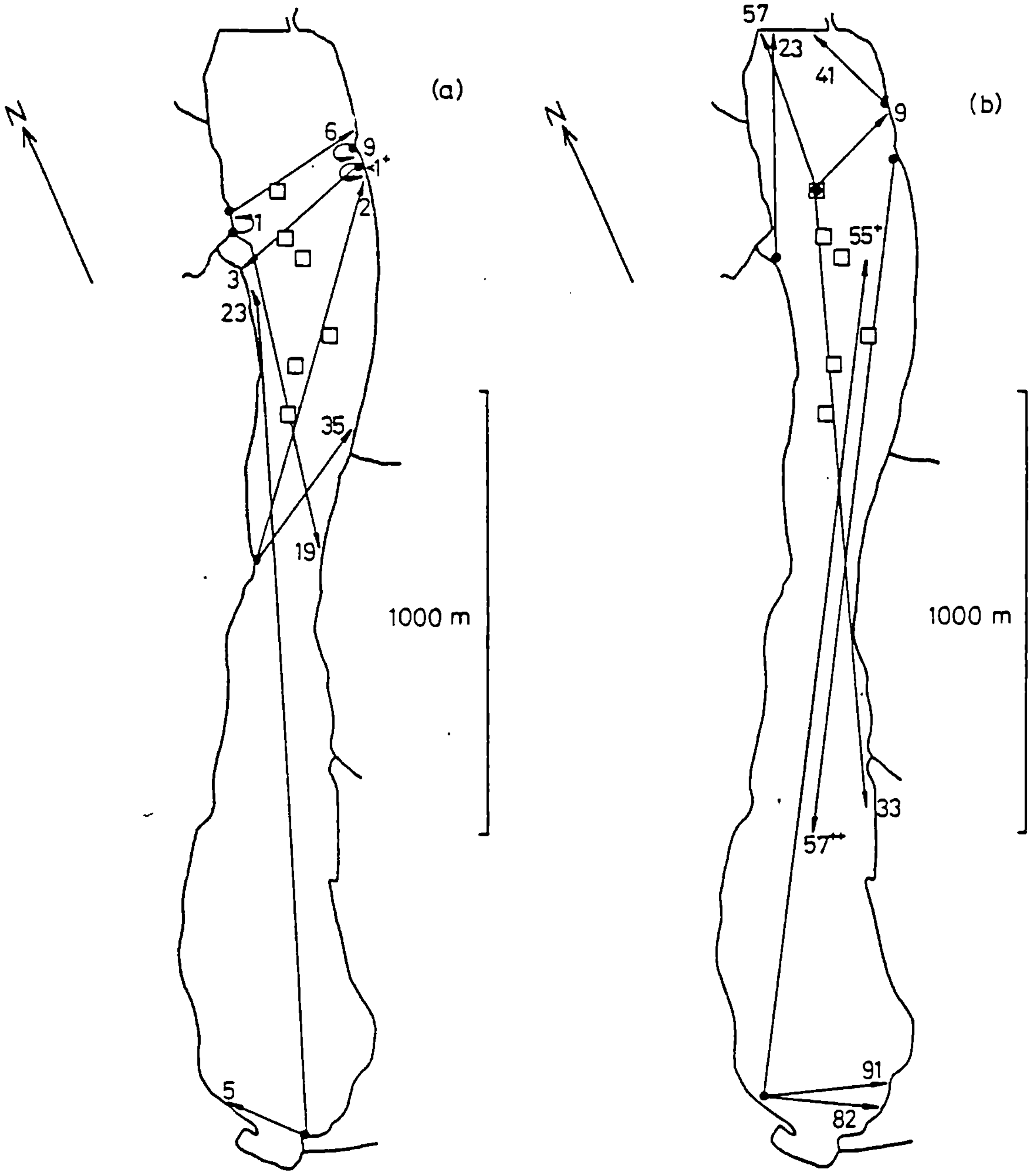
Fish released at R3 moved in both a southerly and northerly direction and, although there were only a small number of returns, this result suggests that there was no tendency to return to the basin in which they were originally caged.

A qualitative comparison of the movements of stocked and naturalized fish tagged at a similar time suggests that naturalized fish were more limited in their short term movements (Figures 3.31, 3.32). A significantly greater proportion of fish stocked from Cage VI (Fisher's exact probability test; $p < 0.05$) were recaptured by anglers within 30 days of release than naturalized fish that were originally captured and released from Cage VI. This result needs to be interpreted with care because the angling pressure may have been different on these two different occasions (Section 3.3.6.3.4.) and naturalized fish showed less affinity for the cages in April (Sections 3.3.6.3.4., 3.3.6.3.6.). If correct though, it shows that stock fish released from the cages were more available to angling than naturalized fish netted from the cages and therefore probably made greater initial post-stocking movements than naturalized fish. This initial activity was similar to the fish released into Loch Charn and similarly, as the stocked fish became naturalized fish, they must therefore have become less active with time.

Figure 3.32. The movements of naturalized rainbow trout captured away from the cages. The time (days) between their release at ● and subsequent recapture is shown adjacent to their recapture point.

(a) shows the movements of fish tagged 27 April - 2 May 1981 (+ indicates two fish with identical movements that were caught at the same time. Only one of these is shown). Fish recaptured by beach seine and anglers.

(b) shows the movements of fish tagged 3-5 June 1981 (+ caught in gill net, ++ caught from boat). All of these fish, except one caught in a gill net, were recaptured by anglers.


(a)
N
6
9
1+
2
1
3
23
35
19
5
1000 m
(b)
N
57
23
41
9
55+
33
57++
91
82
1000 m

Long term recaptures of stocked fish were all by anglers within the northern basin (Figure 3.31b), but this is probably a reflection on the greater fishing pressure in this area and is no evidence for any preference for this basin.

3.3.6.3.3. The movements of naturalized fish captured from the shore

It is apparent from Figure 3.32 that fish caught in the littoral zone moved throughout the northern basin. The following analysis was designed to test the null hypothesis that naturalized fish captured by beach seine also moved randomly throughout the whole loch. If this was the case then, firstly, there should be no significant difference between the proportion of northern and southern fish in all of the tag returns of naturalized fish recaptured in the northern basin. Fisher's exact probability test showed that there was no significant ($p > 0.1$) difference between the return of fish tagged in the north and south basins, showing that the movement of southern fish was not restricted to the southern basin.

This result does not imply littoral fish moved randomly throughout the loch, because it may have been due to a net movement of fish towards the north throughout the sampling period (April - August). Two naturalized fish tagged in the northern basin were, however, recaptured in the southern basin showing that there was some movement out of the former basin. There was also no evidence of a decline in the beach seining catch rate (fish/standard haul) at the southern end (Sites 4,5,6) during the three sampling trips (April/May, 5.14 fish/haul (7 hauls); June, 5.17 fish/haul (6 hauls); July, 23.67 fish/haul (3 hauls)). Thus, there must have been a continual flux of fish into and out of the southern basin to maintain the littoral population at this end of the loch; i.e., movement of littoral fish throughout the loch was probably random between April and August.

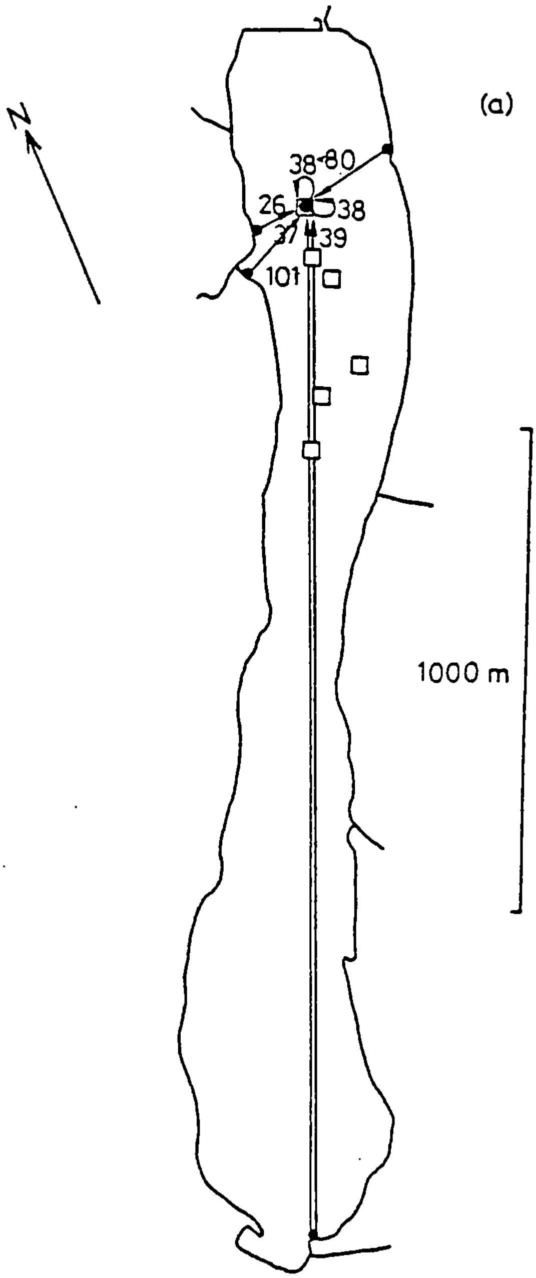
3.3.6.3.4. The movements of naturalized fish captured around the cages

Although littoral caught fish may have moved randomly throughout the loch there was some evidence that naturalized fish at the cages were more

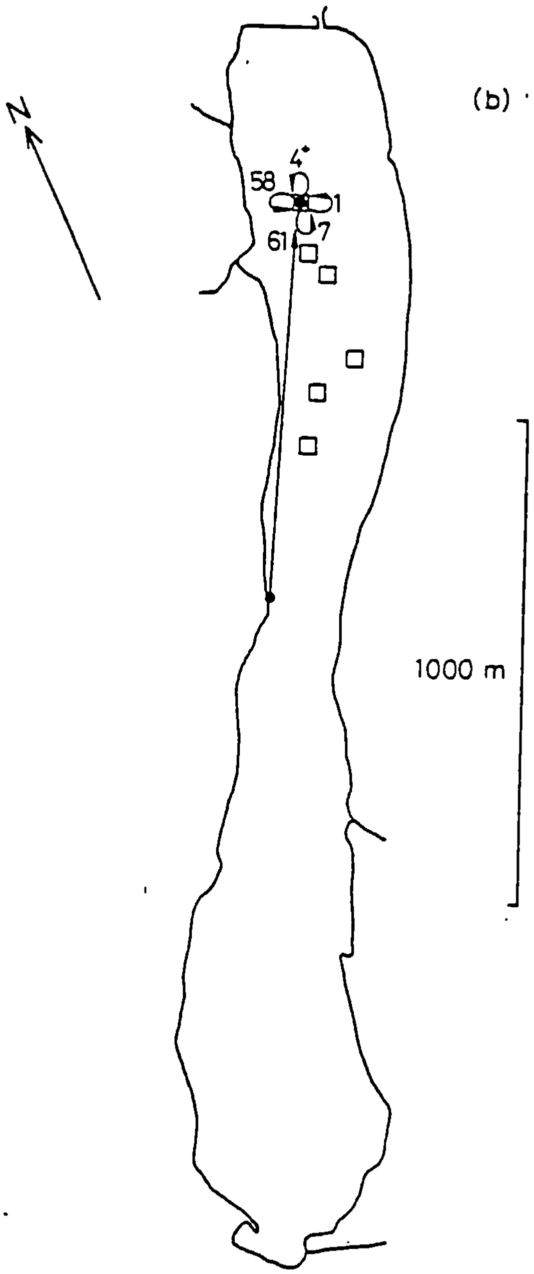
Figure 3.33. The movements of naturalized rainbow trout captured at the cages. The time (days) between their release at ● and recapture at the cages is shown adjacent to their recapture point.

(a) shows the movements of naturalized fish tagged on 27 April -2 May 1981 (< 80; exact date of capture unknown but less than 80 days).

(b) shows the movements of naturalized rainbow trout tagged on 3 - 5 June 1981 (+ represents 3 fish with identical movements, only one of which is shown).



N
(a)
38
80
26
38
37
39
101
1000 m



N
(b)
4
58
1
7
61
1000 m

restricted in their movements after May (Figure 3.33 and Sections 3.3.6.3.6. and 3.3.6.3.8.). Between 28 April and 3 May only seven tagged fish were released from the cages (Table 3.12) and although none of these were recaptured, ultrasonic tagging experiments (Section 3.3.6.3.6.) showed that during this period cage caught fish roamed freely throughout the loch.

In June, 99 tagged fish were released from Cage VI and, although there was no significant difference in the proportion of these and the 40 northern basin shore caught fish tagged during the same sampling period that were recaptured by anglers (Fisher's exact probability test; $p > 0.1$; Figure 3.32b), there was a significantly smaller proportion of the former stock recaptured by anglers within 30 days of release when compared with all the naturalized fish captured and released from the shore of the northern basin (Fisher's exact probability test; $p < 0.05$; Table 3.13). This disparity between results may have been due to a decrease in the angling pressure and a smaller number of returns after June but may also have been a result of some movement from the littoral zone to the cages after this sampling period (which probably occurred; Section 3.3.6.3.7.). If correct, however, the results show that, in June at least, the naturalized fish at the cages were more limited in their distribution and consequently less available to anglers than the littoral stock. Figure 3.33b shows, however, that, even after June, this distribution was not a rigid one because there was some flux of tagged fish between the cages and the shore.

Figure 3.34 shows the movement of naturalized fish captured at the cages and displaced to the southern end. A significantly greater proportion of overall tag returns came from these fish than stocked fish released at R4 (Fisher's exact probability test $p < 0.01$). There was also a significant increase in the proportion occurring in the north basin when compared with the naturalized fish beach seined and tagged at the southern end ($p < 0.05$). Three reasons may be

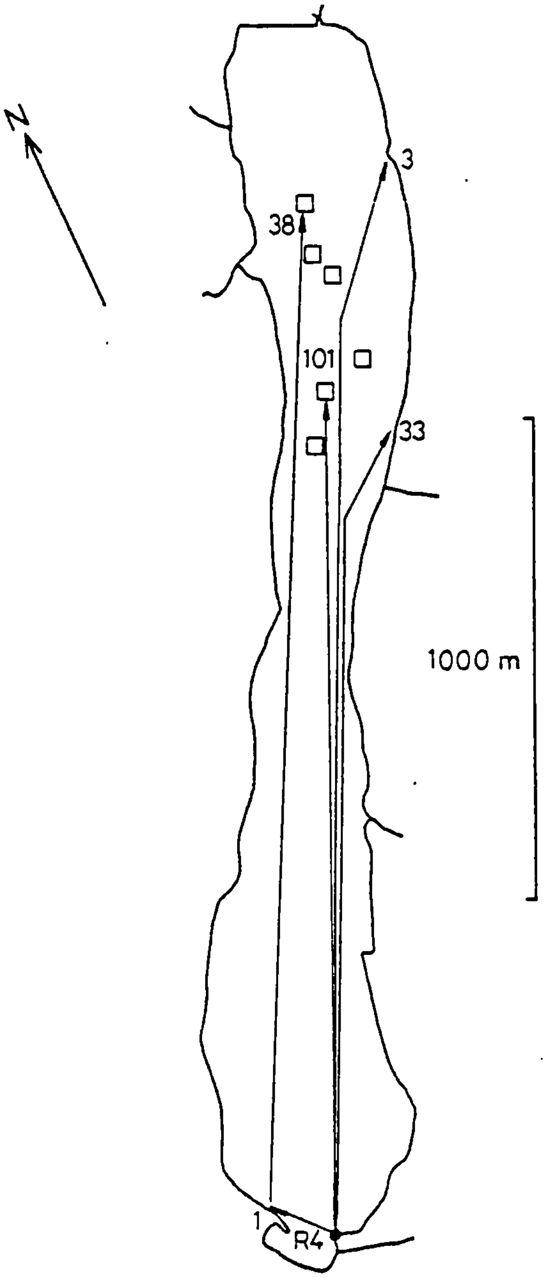


Figure 3.34. The movements of naturalized fish originally captured from around Cage VI but displaced to and released from R4. The time (days) between their release at ● and their subsequent recapture is shown adjacent to their recapture point.

Figure 3.35. The movements of two ultrasonically tagged rainbow trout stocked from Cage II (●).

The fish were located, at the positions indicated, at the following times :

(a) Fish F1 : length 301 mm; weight 375 g

<u>1 May</u>

a. 2335 - released from Cage II (●); a. 2340;

<u>2 May</u>

a. 0000; b. 0130, 0230; c. 0320; d. 0355; e. 0835; f. 0905; g. 1015, subsequently lost

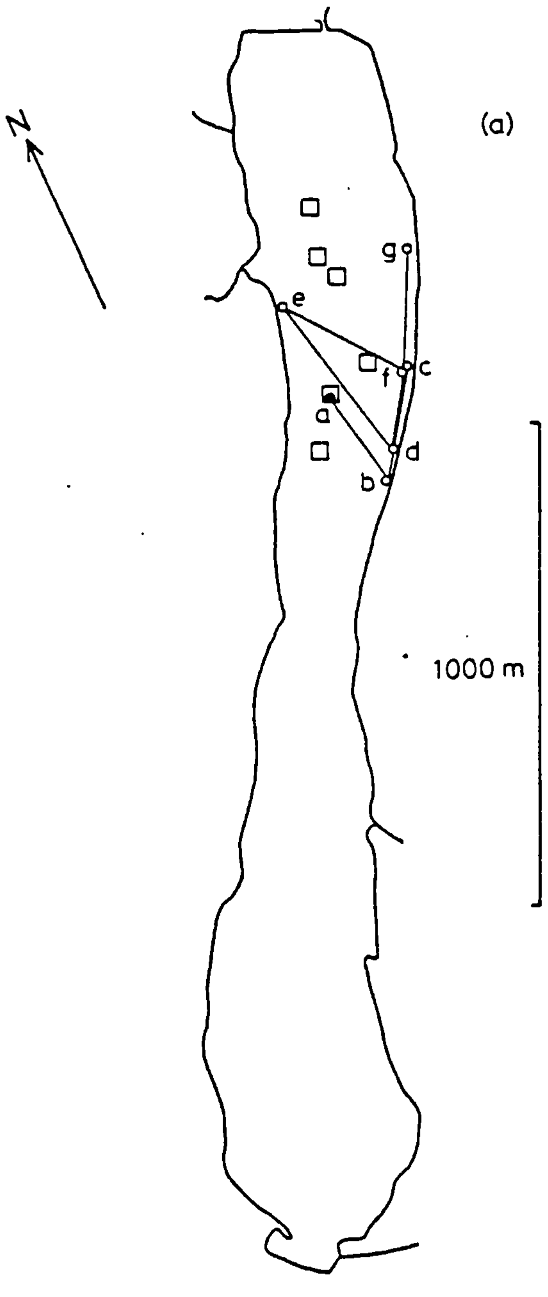
(b) Fish F2 : length 297 mm; weight 320 g

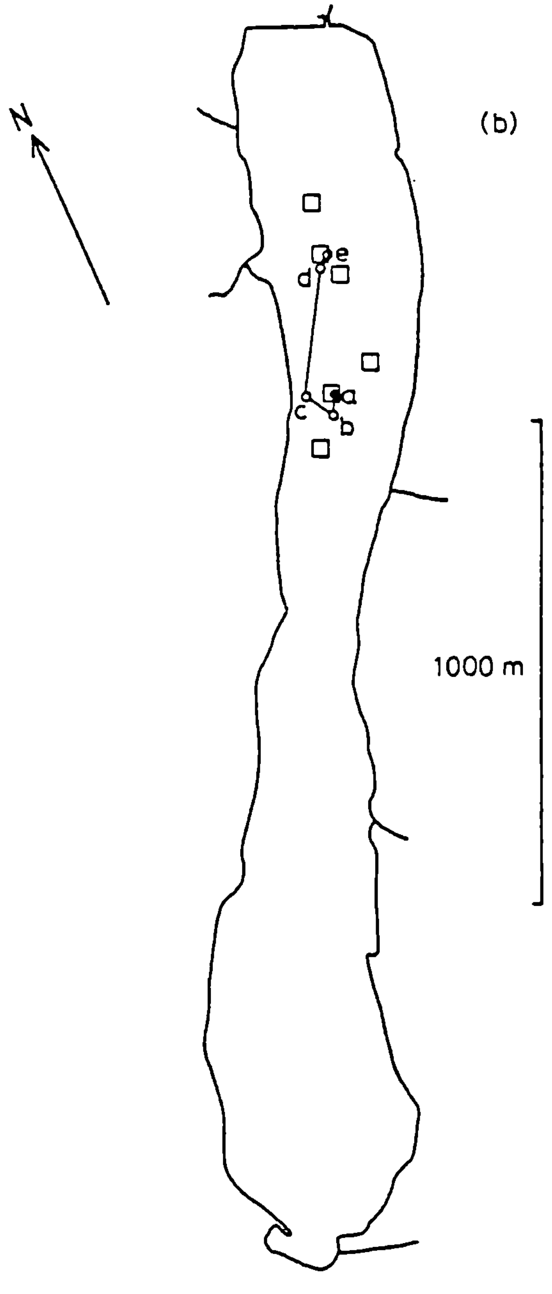
<u>29 April</u>

a. 2100 released from Cage II (●); a. 2105, 2110, 2145, 2305, 2340;

<u>30 April</u>

b. 0020; c. 0140, 0150; d. 0200; e. 0355, 0500, subsequently lost


N
(a)
g
e
c
f
a
d
b
1000 m


N
(b)
e
d
a
c
b
1000 m

proposed for the disproportionate returns when compared with the recently stocked fish; (1) the displaced fish returned to the northern basin quicker than other fish stocked or beach seined in the southern basin, (2) they were larger fish (mean length 377 mm; s.d. = 57 mm; n = 10) and more acclimatised to the loch and may have survived better than the smaller individuals or (3) the returns of the smaller fish may have been underestimated. Further speculation is unwarranted by the small number of tag returns.

3.3.6.3.5. The movements of ultrasonically tagged stocked fish

The movements of stocked fish released from the cages into the loch at Cage II are shown in Figure 3.35. Unfortunately, none of the tags lasted longer than 10.7 h, so the behaviour of both fish would have been influenced by the tagging procedure (Holliday et al., 1974). Neither fish showed the extensive initial exploratory behaviour of the fish released into Loch Charn and both preferred to remain close to their release point for up to 5 h after release. This difference may have been because they were released late in the evening or (most likely) had recently (< 2 h) been tagged. There was no long term preference for remaining near the release point and after 5 h both had moved at least 300 m from Cage II. One fish (F1) moved close to to the shoreline, 2 h after being released, where it remained throughout the rest of the tracking period. The other fish (F2) remained in deeper water closer to the cages until contact was lost. Thus, although the movements of these tagged fish would have been affected by the tagging procedure and was limited to a short tracking period they moved away from their release point as other conventionally tagged fish had done.

3.3.6.3.6. The movements of ultrasonically tagged naturalized fish caught and released outside Cage II

The tracks of the naturalized fish are shown in Figures 3.36 and 3.37. Both fish were tracked over several days beyond the 48-h recovery period

Figure 3.36. The movements of an ultrasonically tagged naturalized fish (F3; length 259 mm; weight 220 g) captured and released at Cage II (●).

The fish was located, at the positions indicated, at the following times :

29 April

a. 2100 released from Cage II; b. 2120; c. 2145; d. 2240, 2300; e. 2350;

30 April

e. 0025, 0120, 0150; f. 0325; g. 0400; h. 0512; i. 0610; j. 0650; k. 0656;

l. 0730;

m. 0815; n. 0848; o. 0910; p. 0950, 1010; q. 1130, subsequently lost;

r. 2125, relocated; r. 2150, subsequently lost;

1 May

s. 2230, relocated; t. 2310;

2 May

t. 0005; u. 0100; v. 0115; w. 0120, 0230; x. 0325, 0348, 0442, 0505; y. 0555;

z. 0640, 0725; a'. 0815; b'. 0825; c'. 0910, subsequently lost;

d'. 1505, relocated; e'. 1622; f'. 1730;

3 May

g'. 1245

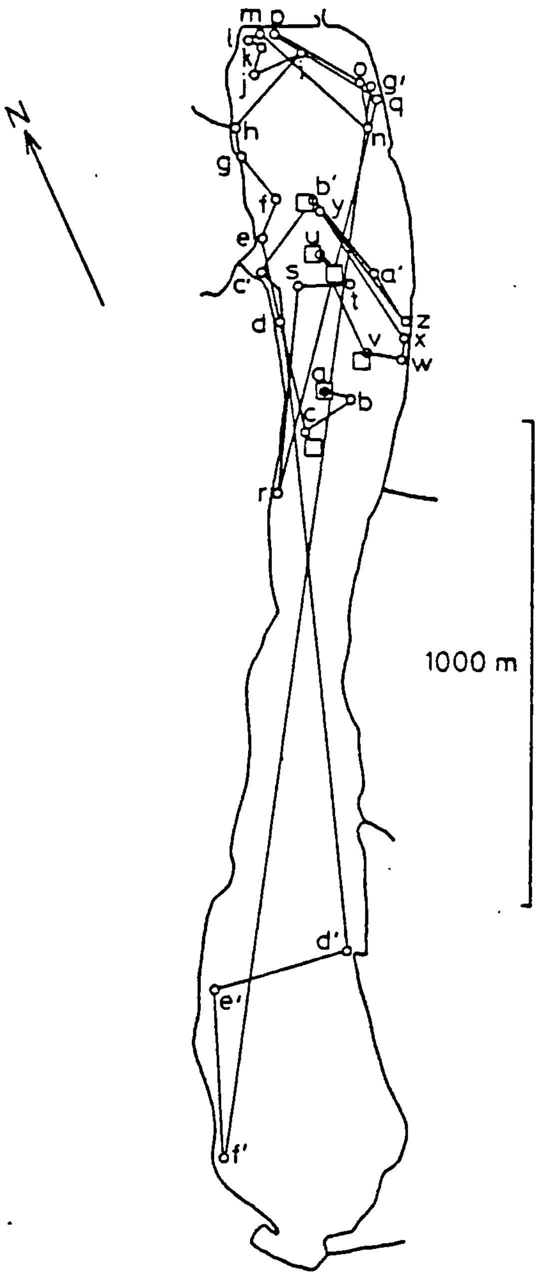

N
m
p
l
k
j
i
o
g'
q
h
n
g
b'
f
y
e
u
a'
c'
s
t
z
x
d
v
w
a
b
c
r
1000 m
d'
e'
f'

Figure 3.37. The movements of a naturalized rainbow trout (F4; length 357 mm) captured and released from Cage II (●).

The fish was located, at the positions indicated, at the following times :

(a) 28 April until 30 April

28 April

a. 2350;

29 April

a. 0025; b. 0050; a. 0105, 0205, 0255, 0350, 0420, 0440;

c. 0500; d. 0540;

e. 0617; f. 0630, 0645; g. 0700, 0730, 0800; h. 0820, 0900; i. 1030, 1100, 1200; j. 1735, 1853, 2000; k. 2050, 2140; l. 2210; m. 2250; n. 2345;

30 April

o. 0020; n. 0115; p. 0200, 0313, 0400; n. 0505, 0600; q. 0705; p. 0740;

q. 0810, 0830, 0930, 1120, 1215; r. 1430; s. 1505, 1700; j. 2115; r. 2200, continued in (b)

(b) 1 May until 3 May

1 May

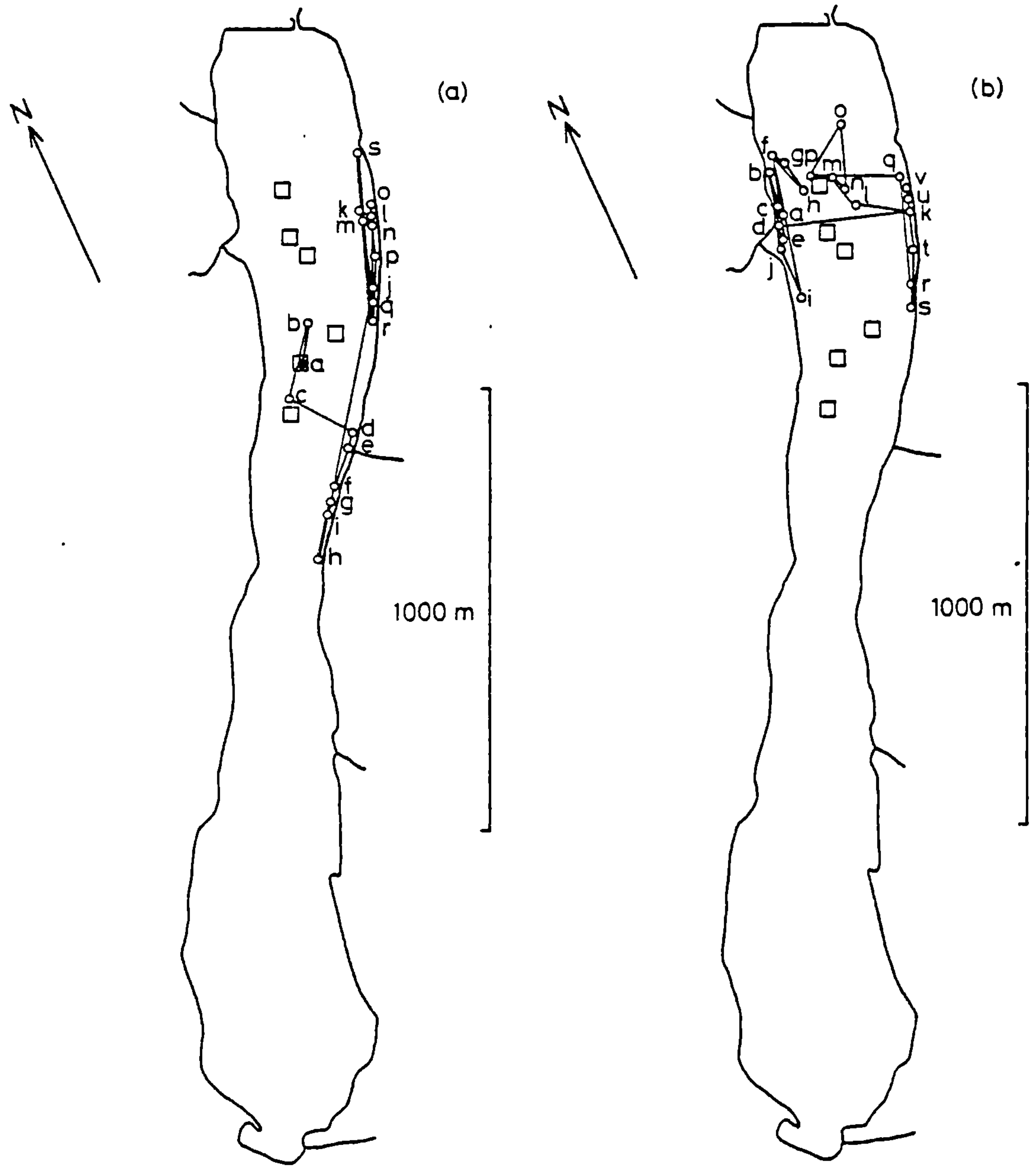
a. 1205; b. 1235; c. 1345; d. 1550; e. 1730; f. 2225; g. 2300;

2 May

h. 0010; f. 0045; i. 0225; j. 0325, 0350; d. 0440, 0505; k. 0550; l. 0648;

m. 0720;

n. 0820; o. 0917; p. 1010; q. 1355; r. 1525; s. 1625; t. 1715; u. 1730, 1830; v. 1240, 1325;



(a)
N
s
o
k
l
m
n
p
j
q
r
b
a
c
d
e
f
g
i
h
1000 m
(b)
N
o
f
g
p
m
q
v
b
n
u
l
c
a
h
k
d
e
t
j
i
r
s
1000 m

(Holliday et al., 1974) and showed no tendency to remain close to Cage II or any other cages. Only fish F4 was at the cages for a short time during the daytime when farm fish were fed (Figure 3.37). Fish F3 spent a small amount of time at the cages, but at night when the caged fish were not fed (Figure 3.36). There was no evidence that these fish were attracted to the cages whilst caged fish were being fed. Thus, although both fish frequented the areas of the cages, they did not remain there for any length of time and there was therefore no evidence that fish were restricted to the area of the cages during this period (28 April - 3 May).

Neither fish were restricted to any particular part of the loch, although both spent most time on the littoral zone in the northern basin. Fish F4 appeared to prefer an area on the eastern shore of the northern basin, returning here after excursions to the cages and the opposite shore. Fish F3 was more active and traversed the length of the loch during observations which, like the conventional tagging results, suggests that fish were not restricted to either the northern or southern basin.

Analysis of feeding behaviour is difficult when one cannot control the food input (as was possible in Loch Charn), or transmit information about feeding events (e.g., Oswald, 1978). Tagged fish were, however, tracked up and down an area of the littoral zone and such behaviour may correspond with a patrolling type of feeding behaviour. No crepuscular patterns of activity emerged from the data although this may have been missed as a result of the long interfix intervals.

3.3.6.3.7. Population structure of the rainbow trout in Loch Fad

Figure 3.38 shows the length frequency distribution of the rainbow trout captured in Loch Fad. There was no significant difference (t test; $p > 0.05$) between the mean fork length of the fish beach seined in the northern and southern basins on each occasion. This result again shows that these two stocks

Figure 3.38. Length/frequency histograms of the rainbow trout captured in Loch Fad on each sampling trip. The upper line on each histogram shows the total fish caught in each size class and the shaded area shows the number of these fish that were caught in the southern basin. The difference between the two gives the number captured in the northern basin.

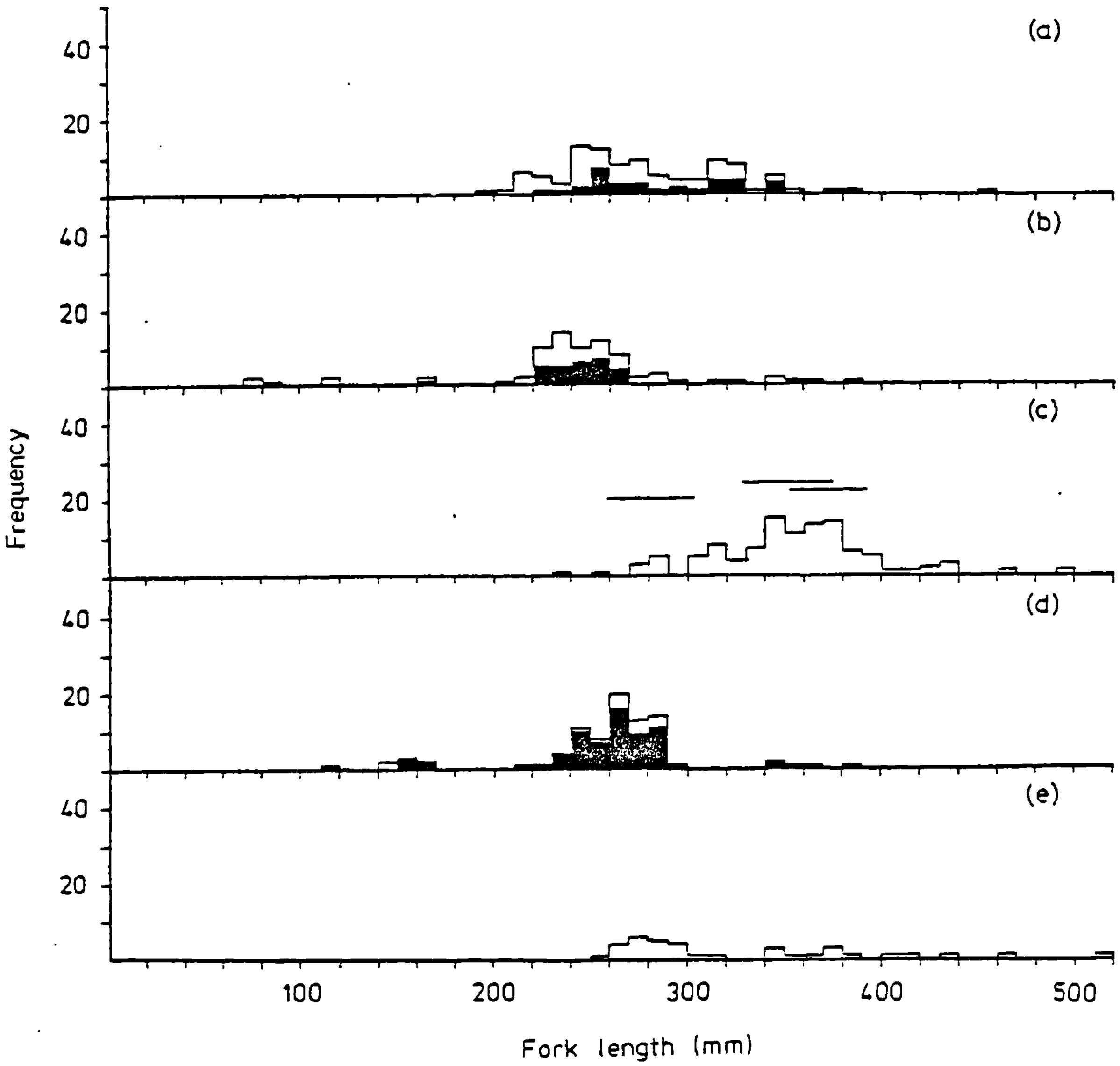
(a) 28 April until 2 May; beach seine caught samples ; n = 98; 21 hauls; $\bar{X} = 278$ mm (s.d. = 46).

(b) 3 June until 5 June; beach seine caught samples; n = 76; 17 hauls; $\bar{X} = 244$ mm (s.d. = 52).

(c) 4 June until 5 June; captured from Cage VI; n = 109; $\bar{X} = 351$ mm (s.d. = 42). Bars indicate growth of 3 tagged fish caught in (a) which were recaptured from Cage VI.

(d) 30 July; captured by beach seine; n = 86; 7 hauls; $\bar{X} = 258$ mm (s.d. = 44).

(e) 30 July; captured from Cage IV; n = 36; $\bar{X} = 324$ mm (s.d. = 64).


(a)
(b)
(c)
(d)
(e)
40
20
Frequency
100
200
300
400
500
Fork length (mm)

may be treated as one and therefore they are combined in the following analyses.

The mean length of the April/May beach seine catches was significantly greater than the June ($d = 4.500$; d.f. = 172; $p < 0.001$) and July ($d = 3.012$; d.f. = 182; $p < 0.01$) catches. Inspection of Figure 3.38 shows that this decrease was a result of both an input of smaller fish into the littoral zone during May and a loss of a large proportion of fish > 300 mm in length. The proportion of these longer fish in the April/May catch was significantly greater than the proportion in the total beach seine catch in June ($\chi^2 = 11.328$; d.f. = 1; $p < 0.001$) and July ($\chi^2 = 17.796$; d.f. = 1; $p < 0.001$) illustrating the loss. Figure 3.38b shows that this loss of larger fish was caused by a net movement offshore to the cages during May and the capture of tagged fish at Cage VI from all over the loch illustrates this movement (Figure 3.33a).

The movement of larger fish to the cages in May resulted in a significant difference between the mean fork lengths of fish found at the cages and at the shore in June ($d = 14.872$; d.f. = 183; $p < 0.001$) which shows that there were two separate populations of fish in the loch at this time. To maintain these populations the two could not have mixed freely and tag returns (Section 3.3.6.3.3.) and stomach analyses (Section 3.3.6.3.9.) suggested that once fish had occupied the area around the cages their movements were relatively restricted to this area.

The mean length of the July beach seine catches was again significantly less than the cage caught fish ($d = 5.653$; d.f. = 120; $p < 0.001$) showing that the subdivision between the two populations, in the two habitats, still existed at this time. There was, however, a significant decrease in the proportion of larger fish (> 300 mm) at the cages in July when compared to June ($\chi^2 = 32.708$; d.f. = 1; $p < 0.001$). This loss of the larger fish may have been a result of sampling from a different cage, although during the intervening period between the June and July sampling trips extensive commercial netting was carried out from all the cages which probably significantly reduced the numbers of larger fish. The resultant increase in the proportion of smaller fish (< 300 mm) may have been due to the recruitment of smaller fish to the cages after some of these larger fish had been cropped.

Although only one fish > 400 mm was caught by the beach seine during all the visits this size of fish were consistently captured at the cages. This result suggests that during daylight hours at least these larger fish may always have been restricted to the cages, although in May, when a greater number of larger fish (> 300 mm) were captured at the shore, shore based anglers captured fish up to 501 mm. Thus, although these larger fish may have been more limited to the areas around the cages they were certainly making some excursions into the littoral zone during May. Unfortunately, there was no data from ultrasonically tagged fish of this size to confirm any different movement pattern between different sized fish.

3.3.6.3.8. Growth rates of Loch Fad rainbow trout

Analysis of growth rate was carried out on eight tagged fish, captured from Cage VI by the author from 4 June to 5 June and on one tagged fish captured by gill net between Cage IV and the shore on 31 July. Rod caught fish were only included in the analysis when they were captured more than 50 days after tagging because the growth increments were considered to be too small and the measuring errors relatively too large for accurate growth measurements before this time. Specific growth rates were then calculated according to the method of Section 3.2.6.

There was a significant negative linear regression between the natural logarithm of the s.g.r. (% body length/day) and the natural logarithm of the initial fork length (L_I, mm) expressed by the equation:

$$\log_e \text{s.g.r.} = 7.063 - 1.499 \log_e L_I$$

$$t = 2.781;\ \text{d.f.} = 17;\ p < 0.05$$

Figure 3.39. The relationship between the natural logs of the specific growth rate and initial length for fish captured in L. Charn (a) and L. Fad (b). The fish captured in L. Fad were categorized as follows :

○ represents naturalized fish captured on 4 June at Cage VI

□ represents stocked fish captured on 4 June at Cage VI

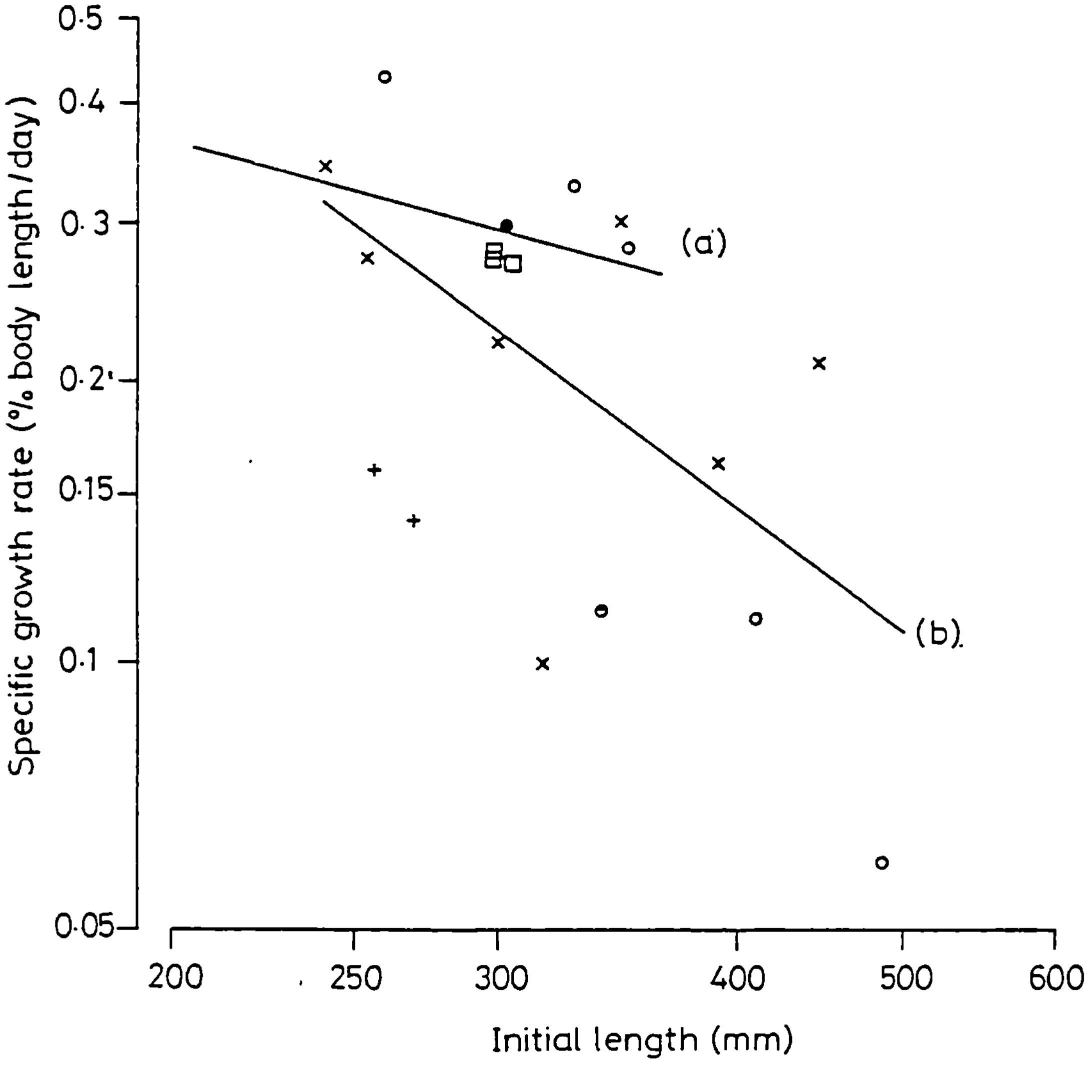
● represents the growth of caged fish between 28 April and 4 June

⊖ represents the growth of caged fish between 4 June and 31 July

X represents naturalized fish captured in the N. basin by anglers after 4 June

\+ represents naturalized fish tagged and captured in the S. basin by anglers after 4 June.

Analysis of covariance (Snedecor and Cochran, 1978) showed that there was a significant increase in the residual variance of line (b) when compared to line (a) ($F = 8.00$; 17 and 35 d.f.; $p < 0.01$). There was, however, no significant difference between the regression coefficients ($d = 0.149$; d.f. $= 21$; $p > 0.10$) (Bailey, 1959).


Specific growth rate (% body length/day)
0·5
0·4
0·3
0·2
0·15
0·1
0·05
(a)
(b)
200
250
300
400
500
600
Initial length (mm)

There was no significant difference between the slope of this line and that derived from the rainbow trout in Loch Charn although there was a significantly greater variation about the line in Loch Fad (Figure 3.39). This greater variation could have arisen from the differences in feeding opportunity in Loch Fad although there were no significant differences between the growth rates of any particular stock, either caged or free-swimming. Variations in water temperature, which could have been related to changes in the eutrophic water quality, may have accounted for some variation in the growth rate of fish caught at different times and the higher temperatures experienced between June and July could have been partly responsible for a decrease in the growth rate of caged fish between these periods (Figure 3.39).

There was probably less variability in Loch Charn because of the more constant food supply because the fish that were used for this analysis had almost certainly been feeding around the feeding station for a considerable time.

3.3.6.3.9. The diet of Loch Fad rainbow trout

A description of the diet of Loch Fad rainbow trout is in preparation by Stirling (pers. comm.). The present report only considers aspects of diet which are relevant to the movements of the naturalized fish at the cages and the littoral zone and how their feeding habits compare with those in Loch Charn. Details of the diet are shown in Table 3.14 and Appendix B.2.

Although the sample was not very large it was apparent that at the beginning of May some fish were feeding both at the cages and in the littoral zone. This behaviour was probably size dependent because of the eight fish whose fork lengths were known, the four largest (450, 450, 459, 501 mm) contained fish farm food and the four smallest (269, 281, 301, 324 mm) did not. This significant difference in diet (Fisher's exact probability test; $p < 0.05$) suggests, therefore, that the larger (> 400 mm) fish were behaving differently

Table 3.14. The relative importance of the three main dietary components of the rainbow trout in L. Fad. The percentage of the total occurrence and dry weight index are shown in brackets. Further details of the animal components are given in Appendix B.2.

Date and position of capture	n	Mean and range of lengths (mm)	Food item	Occurrence (% occurrence)	Dry weight index (% total dry weight index)
1 May. N. basin, E. shore	13	369 (269-501)	Fish farm food	7 (53.85)	27.76 (67.71)
			Plant/detritus	6 (46.15)	1.27 (3.10)
			Animal	7 (100.0)	11.97 (29.19)
5 June. Cage VI	7	363 (340-380)	Fish farm food	7 (100.0)	66 (100.0)
			Plant/detritus	0 (0)	0 (0)
			Animal	0 (0)	0 (0)
30 July. Cage IV	9	381 (274-516)	Fish farm food	9 (100.0)	85.95 (99.94)
			Plant/detritus	1 (11.11)	0.02 (0.02)
			Animal	2 (22.22)	0.03 (0.03)
30 July. N. basin, E. shore	3	270 (265-281)	Fish farm food	0 (0)	0 (0)
			Plant/detritus	2 (66.67)	10.87 (83.62)
			Animal	3 (100.0)	2.13 (16.38)

from the smaller fish and were making excursions between the cages and the littoral zone at this time. The smaller fish showed no evidence of having fed at the cages and therefore, as the beach seining results suggest, they were probably relatively permanent members of the littoral stock at that time of the year.

No fish farm food was seen in any other stomachs or intestines of littoral caught fish after May, although larger fish were not available later in the year. An examination of both the stomachs and intestines of fish up to 382 mm caught in the southern basin also showed no evidence of farm food (Stirling, pers. comm.). Thus, on the basis of stomach contents there was no evidence of short term movement between the cages and this southern site. The suggestion that movement is restricted to the area around the cages in June and July was borne out by the analysis of the stomach contents and intestines of fish captured at the cages during these periods.

Samples of fish around the cage were captured by feeding fish farm food and therefore the relative importance of this item would obviously have been over-estimated. In June, however, there was no natural food found in the stomachs and in only two out of seven fish was any present in the intestines. These items, a small number of chironomid pupae, which would have been taken from midwater or the surface, and a single Sialis lutaria larvae (benthic) were found amongst an abundance of fish farm food and suggest, therefore, that these fish had been feeding around the cages for at least the time taken for the food to pass through the gastro-intestinal tract. At 15°C (June), Grove et al. (1978) found that a 500-g rainbow trout took 50 h to evacuate a 1% body weight meal of trout pellets from its stomach. Natural food items, however, are evacuated more quickly, particularly in the field (Thorpe, 1977). For example, Elliott (1972) showed that 99% of a meal of Gammarus, chironomid larvae and Baetis was evacuated from the stomachs of brown trout in 16.2 h, although some other items took longer. Grove *et al.* (1978) found that the intestinal tract was emptied in approximately double the time for stomach emptying and therefore, although different items would have been digested at different rates, the paucity of natural food within the intestines of these June samples suggests that the fish had been feeding at the cages for approximately the previous 36 h.

In July, at 17°C, the evacuation period would have been less as evacuation rates are known to increase with temperature (Elliott, 1972; Grove *et al.* 1978). The stomach contents were, however, again dominated by fish farm food. The occurrence of a perch, *Perca fluviatilis*, fry and a single chironomid pupa in the stomachs, both of which could again have been consumed near the cages, provided no evidence for littoral feeding. Six out of nine intestines examined in July contained some natural food, although fish farm food was again the dominant component in all of them. Amongst the natural food were chironomid pupae, *Daphnia* sp. and some unidentifiable insect remains which may all have been taken in the water column or at the surface near the cages. In one, 315 mm, fish a single *Valvata piscinalis* was found which were abundant in the stomachs of fish caught in the littoral zone at this time. Such a single occurrence cannot be taken as any evidence of littoral movement so, again, stomach and intestinal analysis suggests that the recent feeding excursions of these fish had probably been confined to the cages.

Stirling (pers. comm.) found *Gammarus*, *Asellus* and some chironomid larvae amongst fish farm food in the stomachs of fish captured below the cages in August and November. This result suggests that there was some flux of fish between the shore and the cages which was also borne out by the capture at the shore and in the southern basin of fish tagged at Cage VI in June (Figure 3.32b).

The composition of the animal component of the diet contrasted markedly with that consumed in Loch Charn. Unlike the Loch Charn fish, those in Loch Fad consumed little terrestrial food but a large proportion of benthic food, of which Gammarus, chironomid larvae and gastropods were a major component (Appendix B.2).

3.3.6.4. A Summary of the work in Loch Fad

The work in the present section has shown that the cages in Loch Fad, which act as supplementary feeding points, have a significant effect on the distribution of the rainbow trout within the loch. The effect was least noticeable at the end of April when ultrasonically tagged fish roamed around the loch and showed no affinity for the cages. Dietary studies at this time showed that some of the largest fish (> 400 mm) were, however, using the cages as a feeding station, although they were also feeding close to the shore together with smaller fish.

Analysis of the tag returns, a large proportion of which came from the April tagging session, suggested that shore caught fish roamed freely around the loch except when they were recruited to the cages. This recruitment occurred during May after which the cages had a more obvious effect on the distribution of the rainbow trout within the loch. After this time the larger fish (> 300 mm) occupied and remained confined to the area close to the cages in a situation that was probably analogous to the behaviour of the rainbow trout around the feeding station in Loch Charn. The net result of this behaviour was that two distinct populations of rainbow trout were formed with the smaller fish being confined to the littoral zone from which they were probably recruited to the cages as feeding opportunities arose there.

The growth rates of the rainbow trout in Loch Fad were similar to, although more variable than, their counterparts in Loch Charn and were similar to those of cage reared stock. The diet of the Loch Fad fish was considerably different from the rainbow trout in Loch Charn with a smaller proportion of terrestrial and surface food being consumed in the former location.

3.4. DISCUSSION

3.4.1. Post-stocking behaviour of rainbow trout

In Loch Charn both ultrasonically tagged fish covered extensive areas of the loch in the 4 h after being non-traumatically released and on subsequent days they were much more localized in their behaviour. Jenkins (1971) also found that the rate of dispersal of rainbow trout introduced into an observation stream was greatest for 4 h immediately following release. Similar extensive forays were also made in Loch Fad because stocked fish were recaptured all over the loch within 48 h of release. Although the trauma associated with tagging may stimulate hyperactivity (Holliday et al., 1974) and thus promote unnatural extensive movements it could not have been responsible for the movement in Loch Charn because fish were left to recover for 48 h after tagging. This trauma may have been responsible for some of the movement in Loch Fad although some untagged, but recognisable, fish were caught throughout the loch within 24 h of release. Widespread short term post-stocking movements are therefore probably typical of rainbow trout stocked in static water. Although no details of the time scale are given, Shetter and Hazzard (1941) also found that stocked rainbow trout distributed themselves throughout some Michigan lakes varying from 5 to 40 acres in size. Hansen and Stauffer (1971) also recorded rainbow trout up to 500 miles from their release point in the Great Lakes.

In a general review, Henderson (1980) suggests that the three consecutive behavioural responses to a new habitat are a relatively "stereotyped" fright response which , he says, usually involves some form of hiding behaviour in inshore fishes, followed by a tentative and then a full exploration of the new environment. The movements of the ultrasonically tagged fish released in Loch Charn did not completely conform to these generalizations. Initially static behaviour, which could be interpreted as a fright response, was observed in Loch Fad where it was probably associated with the recent stress of tagging rather than purely a response to the novel environment. The wide ranging movements also did not conform to the "tentative exploration" proposed by Henderson (1980), although the time scale of these periods probably show considerable inter- and intra-specific variation. These extensive movements, however, are probably a more typical response to a novel environment. For example, Hawkins _et al._ (1974) found that ultrasonically tagged cod, _Gadus morhua_, were most active within 24 h of being released. The fish used were captured on the east coast of Scotland and released into a west coast sea loch after a recovery period and although such behaviour was interpreted as being an adjustment to the buoyancy of the stomach inserted tag, it probably also reflects an element of exploration. Kleerekoper _et al._ (1970) also found that naive goldfish made an initial "grand tour" of a homogeneous tank so that, even in the absence of external variables, wide ranging behaviour is probably the typical response to a novel environment. Kleerekoper _et al._ (1974) also showed that after this initial grand tour the fish settled down to an area - by - area search pattern and although it is not clear whether the behaviour of the Loch Charn fish conformed to this analysis, their exploratory behaviour probably contained elements of such searching. The exploratory behaviour in Loch Charn, unlike the goldfish in a homogeneous tank, would, however, have been strongly modified by other external stimuli.

Wind may affect post-stocking movements because Hansen and Stauffer (1971), in a series of stocking experiments in the Great Lakes, found that an onshore wind kept rainbow trout inshore where they were more vulnerable to predation. In Loch Charn a Force 6 to 7 south-westerly wind was blowing when the ultrasonically tagged fish were stocked, but this did not restrict subsequent movements even though both fish moved off with the wind. These apparently contrasting patterns of movement were probably due to the smaller size of Loch Charn.

Downstream post-stocking movement usually predominates in streams (Jenkins, 1971; Cresswell, 1981) and therefore the presence of a wind driven and natural current moving in a north-easterly direction probably biased movement in this direction. This behaviour may be similar to migrating Atlantic salmon smolts that are wind driven through large Scottish lochs (Thorpe et al., 1981).

Temperature may also influence movements, because in flowing water at least, salmonids are known to undertake greater post-stocking movement in colder water (Cresswell, 1981).

Interactions between both introduced and native stocks probably also affected post-stocking movements. For example, Jenkins (1971) found that shoaling behaviour affected the dispersal of rainbow trout in a stream with large groups undertaking larger excursions than smaller groups or individuals. There was some evidence for rainbow trout feeding in groups during the present study and video tape recordings taken during release showed that individual trout were attracted to larger aggregations of fish. This behaviour may have been a response to stress (Keenleyside, 1955) but would probably have increased the rate of dispersal.

In Loch Charn the extent and consequences of any interaction with the resident brown trout is unknown, although where the stocked fish came into contact with any dominant native fish this interaction would have enhanced post-stocking movement. The large size difference between the rainbow and brown trout may, however, have served to reduce aggressive interactions (Wankowski and Thorpe, 1979), although may well have made the rainbow trout more successful (Gibson, 1980), even though prior residence confers a considerable aggressive advantage on the indigenous stock (Miller, 1958; Payne, 1975) . In Loch Fad, interactions with similar sized resident rainbow trout would have increased the rate of movement of recently stocked fish.

The availability of shelter and particularly food probably played a major role in determining later post-stocking movements and were probably the reason why the shallow north-eastern end of Loch Charn was initially preferred; both shelter and surface food, which were blown into this end by the prevailing winds would have favoured this area. Food must eventually become the most important factor determining movement and, indeed, was shown to be in both Loch Charn and Loch Fad with, at least the larger fish, aggregating at the optimum feeding site.

3.4.2. The development of the response to the feeding station in Loch Charn

Although fish could be attracted to the feeding station very early on in the experiments it was clear that only by continual reinforcement of this movement could the aggregation at the feeding station be improved. Because the fish aggregated at the feeding station after the first feed the second of each pair of feeds would also have helped to reinforce this attraction.

Movement to the feeding station was by means of shifts in the centre of activity in September and was probably similar, although perhaps quicker, in April. Shifts in these preferred areas were not usually seen during daytime, but may have occurred during crepuscular peaks of swimming activity (Ross et al., 1981) or after feeding, although when ultrasonically tagged fish were observed on such occasions they returned to their previously occupied areas. During April this was not always the case, because some fish were remaining closer to the feeder on each successive feed.

The observed occupancy of a home range is also a typical feature of the indigenous brown trout in the slightly larger, but eutrophic, Airthrey Loch (Young et al., 1972; Holliday et al., 1974; Young et al., 1976; Tytler et al., 1978). There was some evidence from the present study that rainbow trout occupied more temporary home ranges than these brown trout, at least until they reached the feeding station. Such behaviour may, however, be typical of recently stocked fish as Winter (1976) found that stocked largemouth bass, Micropterus salmoides, failed to occupy new consistent home ranges and Young et al. (1976) showed that displaced brown trout were more active than indigenous fish within temporary home ranges that they occupied prior to returning to their own home range. Tytler et al. (1978) considered that this active behaviour was due to aggressive interactions with the indigenous fish and thus, in Loch Charn, if the larger rainbow trout were able to outcompete the smaller brown trout because of their size (Gibson, 1980) the shifts must have been due to other factors. Such active behaviour would, however, allow optimal choice of feeding sites and increased familiarity with a variety of sites which may be useful during predator avoidance or inter- or intra-specific competition.

The availability and distribution of food is a major determinant of home range behaviour (Malanin, 1969, in Thorpe, 1974a) and the lack of adequate natural resources in Loch Charn may have caused fish to occupy temporary or large home ranges. The size of these may also have been increased by searching for wind blown surface material which was a major dietary component. The feeding station could also have affected home range behaviour, both by being included in the home range, as eventually occurred, and by making it less essential, or economically viable to feed on, or even defend, alternative natural resources.

One hundred and five days after the April stocking at least 95% of the rainbow trout still remaining in the loch were successfully collected at the feeding station. Anglers would, however, have cropped fish that were not aggregating and so it is uncertain as to whether the feeding station would have collected all the stocked fish without angling pressure. In addition, as ration determined the number of fish aggregating, a 100% ration could have been insufficient to attract all the fish. To check this possibility the experiment needs to be repeated with no angling pressure, although under practical circumstances more of the stock could probably be collected around several feeding stations.

Complications arose in the development of the response to the feeding station in September when fish showed a greater tendency to remain away from the feeding station in the littoral areas than in April. This difference was most likely due to the presence of a predator and fish may have been less vulnerable in these more sheltered inshore areas. There is, however, some evidence from Loch Fad and previous studies (Hatch and Webster, 1961; Fish, 1963) that rainbow trout actually prefer the littoral zone at certain times of the year and Ball and Jones (1962) recorded an increase in the abundance of brown trout on the littoral zone in Llyn Tegid during September. The latter result, however, contradicts that of Thorpe (1974a) who recorded an offshore movement at this time in Loch Leven.

The development of the response to the feeding station would also have been hindered by a reduction in activity (Holliday et al., 1974) and reduced responsiveness to food (Wankowski, 1981) at this time of year. The food pellets were often blown away from the feeder by the wind during this particular experiment which would have also resulted in a poorer tendency to aggregate because the fish were not consistently reinforced in one position.

3.4.3. The aggregation of fish at the feeding station in Loch Charn

The attraction and aggregation of rainbow trout close to the feeding point in Loch Charn represented an accumulation of the fish around the optimum feeding site. In stream aquaria, Chapman and Bjornn (1968) also found that groups of juvenile chinook salmon (Oncorhynchus tshawytscha) aggregated close to the food inlet points and adjusted their distribution in response to changes in the position of those inlets. Mason (1966, in Chapman and Bjornn, 1968) reported a similar result with juvenile coho salmon (O. kisutch). Wilbur and Crumpton (1974), Wilbur (1974, 1978) and Landless (1978) also found that a variety of stillwater species are attracted to supplementary feeding points. Similar aggregations occur under natural conditions because Malanin (1969, in Thorpe, 1974a) points out that the site of the home range depends mainly on forage resources.

In the present experiments there was a distinct group of fish remaining close to the feeding station and the formation of this group would have been enhanced by the provision of a point food source in an oligotrophic water. Such a heterogeneous distribution of food would also have promoted aggression and territory formation (Rubenstein, 1981) and it was therefore not surprising to observe a territorial individual directly below the feeding point. Territoriality was, however, a minor feature of the behaviour of most individuals within the camera's field of view and, as noted in Section 2.3.2.2. and by Keenleyside and Yamamoto (1962) and Landless (1974b), completely broke down during feeding. Individual aggression was, however, observed at non-feeding times and the group at the feeding station was probably analogous to a shoal of stream-dwelling Atlantic salmon juveniles in a low velocity current adjacent to a velocity drop. Here the salmon commonly occupy a shared foraging space and aggression is limited to an area close to each individual (Wankowski and Thorpe, 1979).

Territory formation may have been inhibited by a lack of topographical features which, as Tytler et al. (1978) suggest, are important in the territorial behaviour of lake dwelling brown trout. Landless (1974b) found that a group of five rainbow trout were difficult to keep in a tank unless submerged partitions were included to allow some visual isolation and territory formation. Kalleberg (1958) also showed that the number of Atlantic salmon fry occupying a stream channel could be increased by introducing large boulders which increased the visual isolation between individuals. Thus, the lack of topographical features may have reduced the tendency to form territories but may also have limited the number of fish within the group at the feeding station.

The experiment in which the ration was reduced showed that the size of the group at the feeding station in Loch Charn was regulated by the amount of available food. Similarly, Mason and Chapman (1965) found that the biomass and numbers of juvenile coho salmon (*O.kisutch*) remaining in two stream channels was greater in the channel which had the greatest food supply. Slaney and Northcote (1974) also found that the emigration of rainbow trout from a stream channel was stimulated by a reduction in feeding level.

In the present study, the reduction in the food supply did not change the area covered by the group at the feeding station but it resulted in a decrease in the density of fish within this group. These results are similar to those of Symons (1971) who found that, although a 15-day reduction in food abundance had no significant effect on the density of territorially dominant Atlantic salmon parr in a stream channel, it resulted in an overall decrease in the density of subordinate fish during this period. Thus, the reduction in the ration of food delivered at the feeding station was probably accompanied by a loss of subordinate fish which could have been mediated by aggression (Symons, 1971).

Chapman (1962) also suggests that the aggression of territorially dominant fish causes emigration of the subordinate population and Slaney and Northcote (1974) showed that a reduced ration stimulated aggression in juvenile rainbow trout. Magnuson (1962) also demonstrated that aggression in medaka, *Oryzias latipes*, increased during food deprivation. Even in the absence of aggression a reduced ration could have stimulated fish to leave the feeding area as Keenleyside (1955) and Beukema (1968) found that swimming activity and dispersal of the stickleback, *Gasterosteus aculeatus*, were stimulated by hunger.

Although the group of fish at the feeder was a distinct aggregation within the loch there appeared to be some peripheral members which entered the feeding area late or were counted on the second of each pair of feeds. These fish would have been less likely to have had their behaviour reinforced and were, therefore, more likely to stray and were probably more prone to angling during the early development of the response to the feeding station. Judging by the angling catches, however, these fish did not wander outside the "forbidden" feeding area during the later stages of the response to the feeding station. Such fish may have been subordinate individuals displaced from the prime central feeding sites or just individuals more prone to wandering, although the former probably promoted the latter. Thorpe (1974a) has shown that poorer condition, probably subordinate fish, are displaced from the prime bottom feeding sites in Loch Leven and a wide range of species contain individuals more likely to wander (Kennedy, 1977).

Fish were not uniformly distributed around the feeding station because they entered the camera's field of view from a consistently preferred area. One of the reasons for this distribution was probably that the rainbow trout preferred to remain in groups. It is not clear, however, why this sector was chosen consistently, because the environment was relatively homogenous, being in deep water, they did not aggregate on the slightly shaded side and they did not even prefer the area downstream of the feeder where any uneaten pellets would have drifted.

Although most fish were restricted to the feeding area there was an increase in the density of fish close to the feeding point, possibly in anticipation of feeding and a net movement away from the area after feeding. Such changes must have been accompanied by either a contraction and expansion of the group or a change in the number of individuals around the feeding station with respect to the feeding times. In fact there was evidence for both types of changes which probably occurred concurrently. This behaviour is completely different to that of catfish (Ictalurus punctatus) in the catfish ponds described by Randolph and Clemens (1976 a,b) where individual fish made distinct daily excursions to a supplementary feeding point from a separate home range.

Diel activity rhythms have been well documented in salmonids. Hoar (1942) and Kalleberg (1958) found a diurnal feeding rhythm in Atlantic Salmon (Salmo salar) and brown trout (S. trutta) and Swift (1962) found that naturally feeding caged brown trout showed a diurnal pattern of activity with a peak at dawn. Bachman et al. (1979) demonstrated a crepuscular pattern of activity in unfed laboratory fed S. trutta, although wild brown trout also show a predominantly crepuscular organisation of activity (Young et al., 1972; Holliday et al., 1974; Priede and Young, 1977; Tytler et al., 1978) which is probably related to peaks of feeding activity (Oswald, 1978). Landless (1974b, 1976a) also found that the feeding peaks of demand fed rainbow trout could be correlated with dusk although Eriksson (1978) has shown that, even though activity in S. salar and S. trutta is primarily related to dawn and dusk, there are seasonal changes in this behaviour. The present study shows that rhythmic changes in the pattern of movement may also occur with respect to pre-set feeding times at times other than dawn or dusk.

Davis and Bardach (1965) also found that the killifish, Fundulus heteroclitus, was able to anticipate feeding times if fed at a constant time in relation to a constant light/dark cycle. Similarly, Wankowski (1977) found that laboratory kept Atlantic salmon parr were capable of anticipating an artificial "dawn and dusk" (lights on and off). Priede and Young (1977), however, suggested that, although wild brown trout were capable of anticipating dawn, this anticipation may have been a response to changing light levels rather than a result of any endogenous rhythm. Swift (1964) failed to influence the timing of the peaks of activity of wild caged brown trout by artificial feeding although the timing of these feeds (irregular, once per 2h) would have made it difficult to distinguish any peaks.

If genuine anticipation occurred in Loch Charn then it was probably regulated according to the hypothesis of Davis and Bardach (1965), by "conditioning the act of feeding to an endogenous cue which itself is co-ordinated by the time of feeding or daily changes in light". Although the evidence for an endogenous activity rhythm in salmonids is contradictory (Richardson and McCleave, 1974 and Varanelli and McCleave, 1974, occasionally in total darkness; Bachman et al., 1979, no free-running rhythm in darkness) there is no doubt that rhythmic physiological changes do occur in the absence of light (e.g. photomechanical movements, Douglas, 1982) so that conditioning to an endogenous cue, as proposed in the above hypothesis, could have occurred in Loch Charn.

Other stimuli such as celestial cues (Quinn, 1980) or physiological changes associated with a variation in stomach fullness would have provided additional cues for anticipating feeding times. Adron et al. (1973) and Landless (1974b, 1976a), for example, demonstrated that demand fed rainbow trout showed peaks of feeding activity at approximately 8-h intervals which were correlated with the rate of gastric evacuation and return of appetite (Grove et al., 1978).

The greatest change in the density of fish around the feeder was seen between the evening and morning feeds and, although this decrease may reflect the fact that fish were only conditioned to be fed during daylight hours, the greater rate at which fish left the field of view in the evening suggests that this was not the only factor involved. The minimum densities, at dusk and dawn, and to a lesser degree mid-day, also correspond with naturally occurring peaks of feeding activity (Oswald, 1978) when there is an expansion of the home range of wild brown trout (Holliday et al., 1974). Thus, these minima could have corresponded with some natural feeding over a wider area, although the fish in the field of view late in the evening appeared less, rather than more, active and were therefore probably not feeding.

The decline in density towards dusk could have been due to fish taking up night-time positions. Edmundson et al. (1968), for example, observed stream inhabiting steelhead trout (S.gairdneri) in inshore shallower waters at night. Hoar (1942) reported that steelhead trout were inactive at night, even though both brown and rainbow trout are capable of feeding at night (Jenkins, 1970). Oswald (1978) showed, however, that wild brown trout actually feed at night and Landless (1974b, 1976a) found that self-feeding rainbow trout consumed up to 40% of their daily ration at night. In Loch Charn the lowering of light levels in the evening would have reduced the range over which the fish were able to maintain visual contact between one another and this may have been responsible for a break up of the group, as well as leading to fewer individuals being attracted to feed (as was observed). This phenomenon of a breakdown of shoaling at night has been recorded in a number of shoaling species (Shaw, 1961).

3.4.4. Pre-conditioning and the reaction to the conditioned stimulus

Pre-conditioning of rainbow trout to sound was not a successful technique. There was some evidence that fish were attracted over an unknown, but probably small, distance when other fish were active at the feeding station but there was no evidence of any attraction over greater distances.

Because the visual cues associated with the experimental net were important in mediating the conditioned response (Section 2) the poor success of pre-conditioning may have been due to their absence in Loch Charn. Von Schiller (1949, in Thorpe, 1956) also found that Gambusia affinis was unable to perform a maze swimming task, it had learnt in a small tank, when transferred to a larger tank. If the pre-conditioned fish had to learn to use novel cues then there is little advantage in pre-conditioning and in future, most successful control could be attained by conditioning in situ.

An inability to localize the sound source may also have inhibited the conditioned response. In Section 2 rainbow trout were thought to be able to detect an 180° change in the position of the sound source at distances of up to 11 m, although localisation may not have been possible over the greater distances required in Loch Charn. A directional particle displacement stimulus is required to localize the sound source (Schuijf, 1981) and near the surface or in shallow water this stimulus is moving in a predominately vertical direction (Banner, 1971) which may have made localisation difficult under the experimental conditions. Olsen (1976), however, successfully conditioned saithe to move between feeding stations that were 80 m apart (although he does not state the relevant particle displacement stimuli). Even so, this species is acoustically more specialized than the salmonids (Hawkins and Johnstone, 1978) because its swimbladder is involved in hearing, which both increases its auditory sensitivity and is thought to be used in directional hearing (Schuijf, 1981). Even if conditioned rainbow trout were not capable of such localisation, however, they should have been aroused by the conditioned stimulus, which they didn't appear to be, and learnt to use other cues to locate the feeding station. There was no evidence for this in situ conditioning.

The lack of in situ conditioning was probably due to the reinforcement schedule which was a result of the experimental conditions prevailing in September. The position of the reward in relation to the conditioned stimulus is an important variable in conditioning experiments (Section 2; Sutherland, 1961; Muntz, 1974) and when the food was spread over a wide area away from the source of the conditioned reinforcer, conditioning would have been least effective. If food was inconsistently distributed around the feeder, as a result of the wind, the fish may have heard the stimulus but have been unable to locate the food. There may, therefore, have been a situation of both partial and delayed reinforcement which, as Mackintosh (1974) suggests, also reduces the effectiveness of the conditioned reinforcer (see also the discussion in Section 2).

If fish aggregated in September, as they had done in April, then conditioning would probably have occurred. The good prognosis from the conditioning experiments in Section 2 make it imperative then that these experiments are repeated under more favourable conditions. In these circumstances a louder sound source and more sensitive ultrasonic tracking equipment (e.g. Hawkins et al., 1974), or a sector scanner with a wider field of view than the television camera's (e.g. Chapman et al., 1974) could be used so that a valid assessment of the potential of this conditioning technique can be made. Even though the sound signal was an ineffective attractant during September, however, it was apparent that food was a very potent attractive stimulus.

3.4.5. The attraction of rainbow trout to the feeding station in Loch Charn

Bardach and Villars (1974) define four stages during feeding : (1) arousal, (2) orientation and search, (3) food intake and (4) ingestion. This section only considers the first two, arousal and search, and the stimuli involved in these stages during the attraction of rainbow trout to the feeding station in Loch Charn.

Although final prey location in salmonids is normally mediated by vision (Ali, 1959; Protasov, 1968; Ware, 1973; Wankowski, 1977), visual cues associated with the food could not have been directly responsible for the long distance attraction in Loch Charn.

Olfactory cues could conceivably have stimulated arousal and helped the rainbow trout search for food. Sutterlin (1975), for example, attracted a variety of marine species to the source of some olfactory feeding stimulants. Most work with salmonids has, however, concentrated on the relationship between olfaction and homing (e.g. Hasler et al., 1978) although McBride et al. (1962) found that aqueous extracts of natural food stimulated exploratory behaviour and feeding responses in juvenile sockeye salmon (O.nerka). Yamagishi (1975) also noted that blinded juvenile rainbow trout could feed on artificial food on the bottom of an aquarium, presumably using olfactory cues. There is no other evidence for olfactory attraction, particularly over the distances observed in the present study although, despite this fact, and particularly in view of the known sensitivity of the salmonids' olfactory system, which is used during homing, olfactory mediated arousal and/or searching cannot be discounted. However, as fish were attracted upcurrent of a slow water movement and the olfactory cues associated with artificial pellets are probably less potent than those of natural food it is considered unlikely that olfactory cues were responsible for all the observed behaviour.

Feeding sounds could also have attracted fish to the feeding station. Hashimoto and Maniwa (1967) and Maniwa et al. (1973) suggest that both trout (probably rainbow trout) and pink salmon (O.gorbuscha) respectively may be attracted to feeding sounds. This evidence is discussed in detail in Section 4 where a series of experiments failed to demonstrate that rainbow trout were attracted to feeding noises. These negative results are not definitive and fish could have become conditioned to associate noise at the feeder with food. However, because a large proportion of the feeding noise is above the frequency range of the salmonid hearing system and was inaudible over less of its range than the conditioned stimulus (Section 4) (and certainly in the shallow littoral zone where sound propagation was severely limited by the muddy bottom) it could not have stimulated fish at any great distance from the source. In addition, although fish moved out to feed when others were active at the feeder they also appeared to have ignored earlier activity even when they were in the acoustically more receptive deeper water. This possible attractive stimulus cannot therefore account for all of the results, although it may have been responsible for some shorter range arousal and orientation under quiet ambient noise conditions.

The best hypothesis for the attraction is probably that the rainbow trout were aroused indirectly by the visual stimulus of other individuals feeding or searching for food. There is ample evidence that the visual stimulus of feeding fish facilitates the feeding activity of other members of a group, both in rainbow trout (Section 2 and Landless, 1974b; 1976a) and other species (Keenleyside, 1955; Uematsu, 1971; Olla and Samet, 1974). Therefore, fish feeding at the feeding station could have stimulated the activity of other fish further away who were not able to see the food and these in turn could have excited individuals that were even further from the food. In this way fish could have been aroused at a considerable distance from the source through several intermediary aroused or actively searching individuals. Keenleyside (1955), Protasov (1968) and Brawn (1969) recognised that certain food searching postures or movements in a single fish could stimulate activity in other individuals (e.g. the head down posture in stickleback; Keenleyside, 1955) so that if a rainbow trout was aroused or actively searching for food its behaviour may have been recognised by, and stimulated activity in, other individuals. Griffon vultures use a similar method of food location and locate most of their food indirectly by watching the activities of neighbouring birds (Houston, 1974).

This indirect attraction to the feeding station would be expected to have been erratic and highly dependent on the distribution of the fish within the loch but have been more successful if feeding stimulated activity over a greater area than that over which the food was distributed. This behaviour was observed although it may have been a response to prior experience of the widely dispersed prey which was encountered during this period. Spencer (1939) and Landless (1974b, 1976,a) also found, however, that food stimulates locomotor activity within a tank and Walters (1966) showed that the wavyback skipjack (Euthynnus affinis) increased their swimming speed during feeding. Even so, when fish were feeding over a wide area, on widely dispersed food, it is easier to evoke the above hypothesis because wider ranging movements and greater prey dispersal would have improved the area covered both by the food and the active fish.

The movements in relation to the wind blown food showed how feeding excursions could be controlled by prey distribution. These behavioural responses may also have been modified by previous experience of prey distribution (Beukema, 1968) under these weather conditions and the rate of food location within these excursions (Ware, 1972). Moving along the pathway of wind blown food would have allowed the fish to intercept food items but would also have helped it locate the source of the food perhaps by following a gradient of food distribution. Such searching would, in theory, have allowed the fish to locate the feeding station after feeding over a wider area and may have been partly responsible for the post-feeding aggregations observed during April. The numbers aggregating on these occasions would also have been improved if fish were converging on the feeding station after feeding along several pathways radiating outwards from the feeder. The increase in the number of fish within the camera's field of view could, however, have also been due to an accumulation of fish within the general area and not necessarily just below the feeding station, although the feeder may have been especially attractive when fish rose to the occasional food pellet trapped close to the scaffolding structure.

The ultrasonically tagged fish spent more time near the feeding station when food was more localized, although they occasionally moved outside of the immediate feeding area. This localized behaviour is probably a result of "area restricted searching" (Thomas, 1974) which would again have been modified by previous experience of the food distribution under these conditions. The aggregation of feeding bouts was probably related to the patchy or clumped distribution of the food and group behaviour. Television observations showed that they sometimes originated from one individual drawing attention to a particular area which resulted in an increase in feeding activity (positive feedback, Landless; 1974b) within this area. Such behaviour could facilitate foraging as it has been shown to do in bird flocks (Krebs et al., 1972).

3.4.6. The movements of rainbow trout in loch Fad

In April there was a wide range of sizes of fish within the littoral zone of the loch and the ultrasonically tagged fish showed a preference for this area rather than the area around the cages. There have been no other studies on the patterns of movement of rainbow trout in this country and most research has concentrated on the indigenous brown trout, but the littoral zone is often preferred by lake dwelling salmonids. Thorpe (1974 a), for example, also found that adult brown trout were abundant in the littoral area of Loch Leven during summer, where there was an abundance of Asellus for food. In studies abroad, however, Hatch and Webster (1961) (U.S.A.) and Fish (1963) (New Zealand) found that rainbow trout preferred the littoral zone but Wurtsbaugh et al. (1975) found that in Castle Lake, California, whereas underyearling rainbow trout frequented the littoral zone, the older fish occupied the epilimnion over deeper water. Hansen and Stauffer (1971) suggested that the movements of steelhead trout (S. gairdneri) in the Great Lakes were largely confined to the shore, although Winter (1976) showed that in Western Lake Superior steelheads followed offshore currents and moved offshore after spawning. Crossman (1959), however, found that rainbow trout were not confined to any part of a 985 acre lake in British Columbia, although their summer distribution was determined by the location of shoals of their prey, the redside shiner.

Apart from when the rainbow trout were aggregating at the cages the movement of fish within Loch Fad was also thought to be random which agrees with the work of Crossman (1959). In June, however, there was a contrasting picture with larger fish aggregating and remaining close to the cages. There may have been several explanations for this change.

The temperature increased from 9°C to 15°C between April and June which may have resulted in some offshore movement to deeper water and coincidently to the cages. Ball and Jones (1962), for example, found that the brown trout in Llyn Tegid were moderately abundant in the littoral zone during winter, increased to a maximum in spring and decreased to zero by midsummer. In Loch Leven, however, the population density of brown trout in the littoral areas was high throughout the summer, up to temperatures of around 20°C (Thorpe, 1974a). Thorpe (1974a) considered that the difference between the two lochs was because the clarity of Llyn Tegid may have inhibited inshore movement during daylight hours. Temperature was, therefore, unlikely to have stimulated offshore movement to cooler water in the highly turbid Loch Fad, particularly as this species is known to be much less sensitive than brown trout to both temperature and algal blooms (Taylor, 1978). May (1973), however, found that temperature is the main controller of rainbow trout distribution in Lake Powell, USA, although it only limits the distribution above 23°C.

There was a noticeable movement of 0+ and 1+ age group perch, *Perca fluviatilis*, into the littoral zone of Loch Fad between April and June. Thorpe (1974c), Fraser (1978), and Burrough and Kennedy (1978) have all found some evidence of competitive interactions betwen perch and salmonids and therefore it is conceivable that this influx of perch may have promoted the offshore movement. An explanation on the basis of such an interaction is, however, unwarranted because it seems unlikely that the movement of larger fish would have been affected by an influx of much smaller individuals, particularly as the smaller sizes of rainbow trout remained. Conversely, the smaller perch may only have been able to move in after the larger rainbow trout had left.

An increase in the amount of available food was probably the main factor that increased the number of fish at the cages in June. According to the fish farm manager though, there was no increase in the amount of food that was fed to the fish farm stock between the sampling dates. However, predator nets (mesh size 10cm x 10cm), which were used to protect the caged stock against cormorants and which hung approximately 50 cm outside of the usual nets containing the stock,were removed during this period. This removal would have allowed the naturalized fish better access to the cages and therefore increased the amount of available waste food for consumption. As the amount of available food determines the number of fish at a feeding station (see earlier discussion) this increase would have allowed more fish to accumulate at the cages.

This net offshore movement produced a distribution that was exactly opposite to that described in Loch Leven by Thorpe (1974a). Here, the larger brown trout (> 300 mm) occupied the more favourable littoral regions during summer and the smaller fish were confined to the offshore areas until they were large enough to be recruited to the inshore stock. Both results are analogous, however, because the distribution of the larger fish in the population is positively correlated with the major site of food availability and the distribution of smaller fish is probably restricted by the presence of, and social relations with, larger individuals. Only when the smaller fish are able to compete successfully or the larger fish are removed (e.g. Loch Fad, July) can they be recruited to these more favourable areas.

Once at the cages, movement appeared to be more limited than when the fish were in the littoral zone, which was probably due to the more easily accessible and localized food supply at the cages. These observations also parallel those of Thorpe (1974a) who found that movement from favourable feeding sites was more restricted than from less favourable locations. There was, however, some evidence of a flux of fish between the shore and the cages in Loch Fad which may, perhaps, have been a response to short term changes in food availability.

As large rainbow trout were feeding at the shore and the cages at the beginning of May the response of the fish in Loch Fad to reduced rations may have contrasted with the response in Loch Charn. The response in Loch Charn was probably a loss of subordinate fish from the feeding station and no significant change in the area covered by the remaining group. The response in Loch Fad, however, could have been to stimulate, large fish at least, to move between the feeding station and the shore. Ware (1972) and Hansen (1972, in Ringler, 1979) stimulated predation rates by depriving fish of food and Keenleyside (1955) and Beukema (1968) also found that dispersal and swimming activity were stimulated by hunger. This contrasting result may have been due to the greater productivity of Loch Fad where the benefits of leaving the feeding station to feed on the abundant natural food could have been greater than remaining close to the cages. In Loch Charn, however, which was much less productive, there would have been a greater advantage in remaining close to and defending the feeding point against intruders.

3.4.7. The diet of rainbow trout

In both Loch Charn and Loch Fad there was evidence that rainbow trout were concentrating on supplementary food when they were aggregating at the feeding stations. This was probably because their movements were limited to the feeding points, but may also have been due to selective predation on artificial food as previous feeding experience of a particularly abundant item, increases future selective predation on that item even though fish will still continue to ingest small amounts of other food items (Ringler, 1979). Appetite may also have played a role in selectivity as Ivlev (1961) concluded that satiation increased the selectivity of carp (Cyprinus carpio), although Ringler (1979) was unable to detect any effect of hunger on prey selectivity in brown trout.

In Loch Charn, surface food was overwhelmingly the most abundant item consumed, although deliberately feeding floating food could have predisposed the fish to feed on surface food. Ringler (1979), for example, showed that brown trout altered the relative time spent searching particular areas in response to previous prey distributions. This bias has also been demonstrated in a practical way by Spataru et al. (1980) who found that when supplementary food was available at the surface for pond reared carp, Cyprinus carpio, they fed predominantly on surface organisms. This feeding behaviour was in marked contrast to their habits in ponds without supplementary feeding where a greater proportion of benthic organisms were consumed.

Surface food also formed an important component of the few brown trout examined and therefore, although the method of supplementary feeding probably predisposed feeding on this item, it was obviously an important component of the diet of salmonids in Loch Charn. A large proportion of this diet was of terrestrial origin which was very poorly represented in the stomachs of rainbow trout in Loch Fad and also in the stomachs of rainbow trout in the productive Hanningfield reservoir (Wootten, 1972). This contrasting result is probably due to the greater productivity and abundance of natural aquatic food in the latter two waters, for as Southern (1935) and Ellis and Gowing (1957) have shown, the relative importance of terrestrial food is usually inversely related to the productivity of the water. Brook trout (Salvelinus fontinalis) have also been known to switch to terrestrial fauna when aquatic fauna becomes less abundant (Allan, 1981). The limited littoral zone in Loch Charn would also have predisposed fish to take less littoral food. The advantage of using terrestrial food, however, is that it is not dependent on the immediate productivity of the water (Norlin, 1967) and it is easily accessible because it is silhouetted against the sky.

Terrestrial food has been found to be an important component of the diet of rainbow trout in some other still water studies (Wurtsbaugh et al., 1975), particularly when the fish live offshore (Swift, 1970; Winter, 1976). The importance of terrestrial food in the diet of salmonids is reviewed by Hunt (1975) and although a diversity of terrestrial insects have been recorded (Macan et al., 1966) Diptera, Hymenoptera, Coleoptera and Hemiptera are the most abundant orders (Hunt, 1975). This was also the case in Loch Charn. Such items, although of minor importance when compared to artificial food, would have contributed to the diet.

Chironomid pupae and pupal cases were the major component of the aquatic fauna taken in Loch Charn. These items become easily available during emergence and were also a common component of the diet in Loch Fad as they are in other lacustrine rainbow trout (Wootten, 1972) and other salmonid populations (Pedley and Jones, 1978). Other aquatic items were of minor importance in Loch Charn but amphipods were an important dietary component in Loch Fad and in other rainbow trout (Bernard and Holmstrom, 1978) and brown trout (Hunt and Jones, 1972) populations. This food source was absent in Loch Charn which, as Campbell (1971) suggests, may limit brown trout production. Molluscs were also an important food in Loch Fad and have been reported as the major item taken by the rainbow trout in Hanningfield reservoir (Wootten, 1972). The trout in Loch Charn and Loch Fad consumed vegetation and, although they are capable of a small amount of cellulose digestion (Lindsay and Harris, 1980), this material is unlikely to have made any significant contribution to the diet. This component has also been recorded in other studies (Swift, 1970; Jeppson, 1972) and although a large proportion was probably taken accidentially during feeding, in Loch Charn, at least, some may have been taken in mistake for artificial food.

3.4.8. The return and growth of stocked fish

The estimated 77.3% return from the 188 rainbow trout stocked into Loch Charn during April 1980 compares well with the mean return of 48.5% (range 14.3 -83.9%; n = 9) for brown trout and 60.4% (range 39.6 - 79.2%; n = 8) for rainbow trout stocked into lowland reservoirs (range of the average sizes of stocked fish; 250 -330 mm) (Crisp and Mann, 1977). This figure also falls within the range of returns of between 76 and 93% (mean 84.02%; n = 4) given by the authors for rainbow trout stocked into less productive upland waters. In these latter waters, although there may be greater returns in terms of numbers, the return in terms of weight (weight of fish caught ÷ weight of fish stocked) is usually much less than the more productive waters for a similar stocking regime (upland; mean = 83.5%; range 79.0 - 86.7%; n = 3; lowland; mean = 140.6%; range 63.5 -264.3%; n = 6) (Crisp and Mann, 1977). In Loch Charn the percent return in terms of weight was approximately 145% (94.32kg/65.05kg) which is greater than any of the aforementioned upland figures and the mean of the lowland figures. This good percent weight return can be attributed to supplementary feeding and the maintenance of a feeding area where fish could grow without being caught by anglers.

The low return (in terms of numbers) from the September stocking (18.0%) was partly due to predation by the cormorant, although may also have been a result of other overwintering mortality which often occurs where rainbow trout are overstocked with respect to the winter food supply (Brown, 1970). The poor overwintering survival of 4.1% compares with that of between 2.03 and 28.9% (mean = 14.42%; n = 7) for underyearling rainbow trout stocked into some N.

Ireland lakes during Autumn (Cragg-Hine, 1975). It was originally hoped to investigate whether supplementary feeding could be used to alleviate such high overwintering mortalities because Mason (1974) found that even supplementary feeding before winter led to a 2 to 3 fold increase in the lipid reserves of coho salmon when compared to unfed stream controls. Unfortunately this plan was abandoned as a result of the adverse experimental conditions, in particular the cormorant.

Predation, as Mundie and Mounce (1978) and Mundie (1980) also discovered, may be a major problem in any extensive farming enterprise. In addition, in all the present experiments, mortality could have arisen from tagging (Eisner and Ritter, 1979) and predation of the April stock may have been slightly enhanced by using yellow tags (Larsson, 1979). Brown (1970) and Hunt and Jones (1972b) also suggest that stocked rainbow trout commonly escape through feeder streams and outlets and, although no fish were ever reported outside of the loch, some may have been lost in this manner.

There was a peak in the number of returns within one month of the April 1980 stocking which corresponded with a less localized phase of behaviour and perhaps a cropping of the fish which had less of a tendency to aggregate around the feeding station. This initial post-stocking surge in the number of recaptured fish is a typical result (Cragg-Hine, 1976; Cresswell and Williams, 1979) which may also be biased by an increased fishing effort during this period (Cresswell and Williams, 1979).

Only 13.57% of the tagged rainbow trout were returned from Loch Fad. This return must be considered as a minimum value, however, because it only represents data from a 4 month period and the special distribution of fish in the loch put a large proportion out of reach of anglers up until August.

Judging by the small size of the brown trout, the small proportion of natural food in the stomachs of the rainbow trout and the decline in the specific growth rate after supplementary feeding ceased, the addition of artificial food was essential to maintain the growth rates of the rainbow trout in Loch Charn. Although Campbell (1971) and Jensen (1977) have suggested that in the absence of supplementary feeding, the growth of populations of lacustrine salmonids is density dependent, the size of the population around the feeding station was determined by the amount of available food and therefore the growth of this population was not strictly density dependent. This type of regulation of population density, which could conceivably occur in natural lake populations around localized food resources, is analogous to the population dynamics of juvenile stream salmonids where density dependent mortality and dispersal resulting from territoriality ensure that a relatively constant number of fry are recruited to a given area of fry rearing ground (Le Cren, 1973).

The observed growth rates must be taken as minimum values because, although Templeton (1971) could find no significant difference between the growth of tagged and untagged brown trout marked with a disc tag inserted through the dorsal musculature, the smolt tag used in the present study depresses the growth rate of Atlantic salmon smolts (Eisner and Ritter, 1979).

In both Loch Charn and Loch Fad the growth rate was found to decline with increasing size which agrees with the work of Elliot (1975) with brown trout, Bernard and Holmstrom (1978) with rainbow trout and the growth models produced by Iwama and Tautz (1981).

The mean s.g.r. of rainbow trout in Loch Charn was 0.300% of body length/day. Cragg-Hine (1976) reports that the maximum growth rate of rainbow trout, in several N. Ireland lakes, was from 308 mm in June to 354 mm in August. He gives no details of the time scale although, if one assumes the time difference is 62 days, a maximum estimate of the specific growth rate would be 0.224% body length/day. This figure is lower than the mean s.g.r. of the fish in Loch Charn over a similar period which, given the rations used, should be comparable to similarly sized farmed fish.

Jarrams et al. (1980) found that rainbow trout grown in freshwater cages between July and September had a specific growth rate of 0.482% body length/day. This growth rate is greater than that of the fish in Loch Charn although the smaller fish used during Jarram et al.'s experiments (103 -145 mm) would be expected to have greater growth rates because of their size. The growth rate of the Loch Charn fish was similar to those in Loch Fad where the growth of naturalized fish was not significantly different from that of the caged stock but there is no other published information on the growth rate of similar sized farmed fish and under similar physical conditions to those in Loch Charn. Iwama and Tautz (1981), however, present an equation modelling growth rate in hatcheries of:

$$Wt^{0.33} = Wo^{0.33} + (T/1000)t$$

where Wt = weight at time t (g)

Wo = initial weight (g)

T = average temperature ($^{\circ}$C)

Substituting values of $Wo = 340$ g (mean initial stocking weight of fish surviving for 110 days after stocking; $n = 39$) and $T = 15.5^{\circ}$ (mean temperature over 110 days after stocking), this equation gives a final weight of 667 g which may be expected under "normal hatchery conditions" at this temperature. This gives a s.g.r. in terms of weight of 0.613%/day and using the length/weight relationship of these fish at stocking it converts to a s.g.r. in terms of length of 0.217%/day. Iwama and Tautz (1981) suggest that their equation predicts to within ± 10 to 20% of the final weight of a stock of hatchery reared rainbow trout. Therefore, as the Loch Charn fish had a mean s.g.r. of $0.300\%.\text{day}^{-1}$ this comparison suggests the fish in Loch Charn were growing better than that observed in previous hatchery growth studies. In summary, considering the results from Loch Fad and Loch Charn, growth rates similar to, or greater than, farmed fish may be obtained under similar "free ranging" conditions.

3.4.9. Brown trout

Small numbers of brown trout, Salmo trutta, also learnt to feed at the feeding station. Ware (1971) has shown that salmonids develop "searching images" which enable them to concentrate on particular prey items. They take time (4 days at 6 food particles per day in Ware, 1971) to learn about novel prey such as the artificial food used in Loch Charn, although a low abundance of natural food may help to promote feeding on this food. This behaviour would undoubtedly stimulate the growth of the brown trout in Loch Charn, though, if taken to extremes, could result in an under-utilisation of natural food as has been discussed for rainbow trout.

There was some evidence that brown trout were co-existing with rainbow trout at the feeder, although it was obvious that only a small number of the former species were involved. Gibson (1980) found that rainbow trout were the most aggressive of a range of similar sized salmonids although brown trout were not included. Wild salmonids are usually more aggressive under natural conditions than hatchery reared stock (Fenderson and Carpenter, 1971), although Gibson (1980) suggests that larger fish are more likely to compete most successfully. If this was the case, then the brown trout would have been less successful at the feeding station, although the large size differences between the two species could have helped to minimize aggressive interactions (Wankowski and Thorpe, 1979). If food became limiting, however, then the brown trout would have probably been outcompeted. When co-existing there may have been an interspecific hierarchy which Fisler (1977) also described for some terrestrial birds and mammals at an artificial feeding station.

Although competitive interactions could have limited the number of brown trout aggregating at the feeder, there may be other differences in their behaviour which may have limited their movement towards the feeding point. Brown trout are usually thought of as solitary individuals (Tytler et al., 1978) and there was evidence from the present study that rainbow trout are a more social species. Brown trout may also be more territorial than the introduced rainbow trout, particularly in Loch Charn where they were smaller and probably fed more efficiently than introduced fish (Sosiak et al. 1979), which may have allowed them to gain sufficient food from a more limited area than the rainbow trout. There may also be interspecific differences in feeding behaviour such as Hyatt (1979) described between rainbow trout and another salmonid species, the kokanee (O. nerka). In Loch Charn there was also some evidence that brown trout remained in specific areas and were not attracted to the feeding station during the early development of the response to the feeding station.

During several observation periods during April, whilst rainbow trout were actively feeding at the feeding station, several brown trout were noticed rising to surface insects close to the shore and approximately 10 m away. There was no observable change in both the timing or pattern of these rises in response to the rainbow trout, suggesting that at this time these brown trout were not attracted to the feeding point.

Outwith the feeding area the two species could compete for food because the natural dietary components of the few brown trout examined were similar to those of rainbow trout. Wootten (1972) found little difference in the diet of brown and rainbow trout in Hanningfield reservoir, although fish were more abundant within the stomachs of the brown trout. De Filby (1976), however, recorded a greater proportion of benthic organisms in the stomachs of a small sample of brown trout when compared to rainbow trout. Thus, some competitive interactions and also differences in behaviour may exist, although further predictions of the interactions are not possible with the paucity of data on the subject.

SECTION 4

THE ROLE OF FEEDING SOUNDS IN THE FEEDING BEHAVIOUR OF RAINBOW TROUT

4.1. INTRODUCTION

According to Stober (1969), Neproshin (1972) and Neproshin and Kulikova (1975), salmonids have an extensive repertoire of sounds. These are associated with the movement of the fish, of air within the fish, of the swim bladder and of the jaws (Neproshin and Kulikova 1975). Winn (1964) and Tavolga (1977) give general reviews of the production and significance of sound production in a variety of fish species. The significance of salmonid sounds is unknown, although Neproshin (1972) suggests that some of the noises may be used during courtship.

A considerable variety of noises have been recorded from feeding fish (Protasov, 1965) and recordings of the sounds of conspecifics feeding have been successfully used to attract yellowtail (Seriola quinqueradiata), mackerel (Scomber japonicus) and jack mackerel (Trachurus japonicus) in some Japanese fisheries (Hashimoto and Maniwa, 1967; 1971; Maniwa et al. 1973; Maniwa, 1976). Kim (1977) also found that yellowtail were attracted to their own feeding sounds and Moulton (1960) showed that the sounds of Anchoviella provoked an excited response in a predator, Caranx. Westenberg (1952) and Moulton (1964) describe a variety of lures used in some primitive fisheries whose success supposedly lies in their imitation of prey feeding sounds.

Hashimoto and Maniwa (1967) mention that trout, probably rainbow trout, were successfully attracted along with carp and dace to recordings of feeding carp. As the lower frequency limit of their transducer (500 Hz) was outside of the audible range of salmonids (Hawkins and Johnstone, 1978), the visual stimulus of other fish (members of the Cyprinidae which are capable of hearing such sounds (Hawkins, 1973)) was probably the attractive stimulus in this study. The only other evidence that salmonids may be attracted by feeding noises is provided by Maniwa et al. (1973) who suggested that the catch of pink salmon (O. gorbuscha) in a stationary net was enhanced in the presence of their "swimming and bait eating" sounds.

The purpose of the present work was to determine 1) what noises are made during the feeding of salmonids, 2) which components of the signals are audible and 3) whether rainbow trout are attracted to the sounds of other feeding fish.

4.2. MATERIALS AND METHODS

4.2.1. Experimental animals and location

Recordings of feeding noises were made from both Atlantic salmon (S. salar) and rainbow trout (S. gairdneri). Rainbow trout from 50 to 500 g and salmon from 1000 to 2000 g in weight were used in these experiments. These fish were held in 3.5 m x 3.5 m x 3.5 m nets attached to rafts moored in Dunstaffnage and Saulmore Bay (Section 2.2.1.). Playback experiments were carried out in Dunstaffnage Bay.

4.2.2. Instrumentation and experimental techique

4.2.2.1. Recording

A calibrated hydrophone (Plessey, MS83) which fed a built-in preamplifier and then a portable tape recorder (Uher 4000 Report Monitor) were used for recording. Recordings were made at a tape speed of 19 $cm.s^{-1}$ which gave an overall frequency response of 20-25,000 Hz. Recordings were calibrated by recording pure tone stimuli of known amplitude and measuring their level upon playback.

The hydrophone occupied a standard position at a depth of 1 m outside the net and approximately 1 m from the centre of feeding activity. If it was placed closer to the fish it was continually knocked during recording. Both floating and sinking food were fed to the fish on separate occasions during the recordings.

4.2.2.2. Analysis

Sound spectrograms of the sounds associated with feeding were prepared by replaying tape recordings into a spectrum analyser (Kay, type 7029A). They represent changes in the frequency spectrum with time and the relative amplitude of the components are indicated by the degree of blackening of the paper. Sounds within the frequency range 20 - 16,000 Hz were examined at a filter bandwidth of 300 Hz.

In addition, frequency analysis was carried out by playback of the recorded signals via an octave filter set (Bruel and Kjaer, type 1613) to a calibrated oscilloscope. Sound levels were expressed in terms of decibels relative to one microbar (dB//1 µbar) either as a broad band level or spectrum level (i.e., the sound level in a band 1 Hz wide) (See Section 2.2.3.).

4.2.2.3. Playback

Sounds were played back to the fish via the amplifier and J9 loudspeaker described in Section 2.2.2. This apparatus gave a flat frequency response over the range 50-25,000 Hz. Playback was adjusted to the recorded level at a distance of 1 m from the source and occasionally + 10 dB above this level.

Preliminary experiments were carried out with fifty, 500 g rainbow trout in a 17 m x 3.5 m x 3.5 m net with the loudspeaker at a depth of 1 m and 2 m from one end of the cage. Later experiments were carried out with one hundred, 50 g fish in a 2 m x 2 m x 2 m net with the loudspeaker at a variety of depths from the surface to 1 m.

Responses were recorded on video tape using the underwater television described in Section 2.2.2. with the camera pointing vertically upwards from near the bottom of each cage.

4.3. RESULTS

4.3.1. Feeding noises

The dominant component of the feeding noises of both rainbow trout and Atlantic salmon was the splashing associated with surface feeding. Noise originated as the fish broke the surface to take the food and left the surface with a strong tail flip. Figure 4.1(a) is a sonogram of the noise associated with food pellets striking the water followed by two approximately 500-g rainbow trout rising to food. The transient nature of the noises associated with the splashing is clearly evident from this sonogram. The sound energy extends from 20 Hz to 2,000 Hz in this sonogram, but was found to extend up to at least 16,000 Hz in others. Figure 4.2 is a spectral analysis of four rises which also shows that these noises cover a wide frequency range. A large portion of this energy is above 400 Hz and would therefore be inaudible to salmonids (Section 2.3.2.9.; Hawkins and Johnstone, 1978).

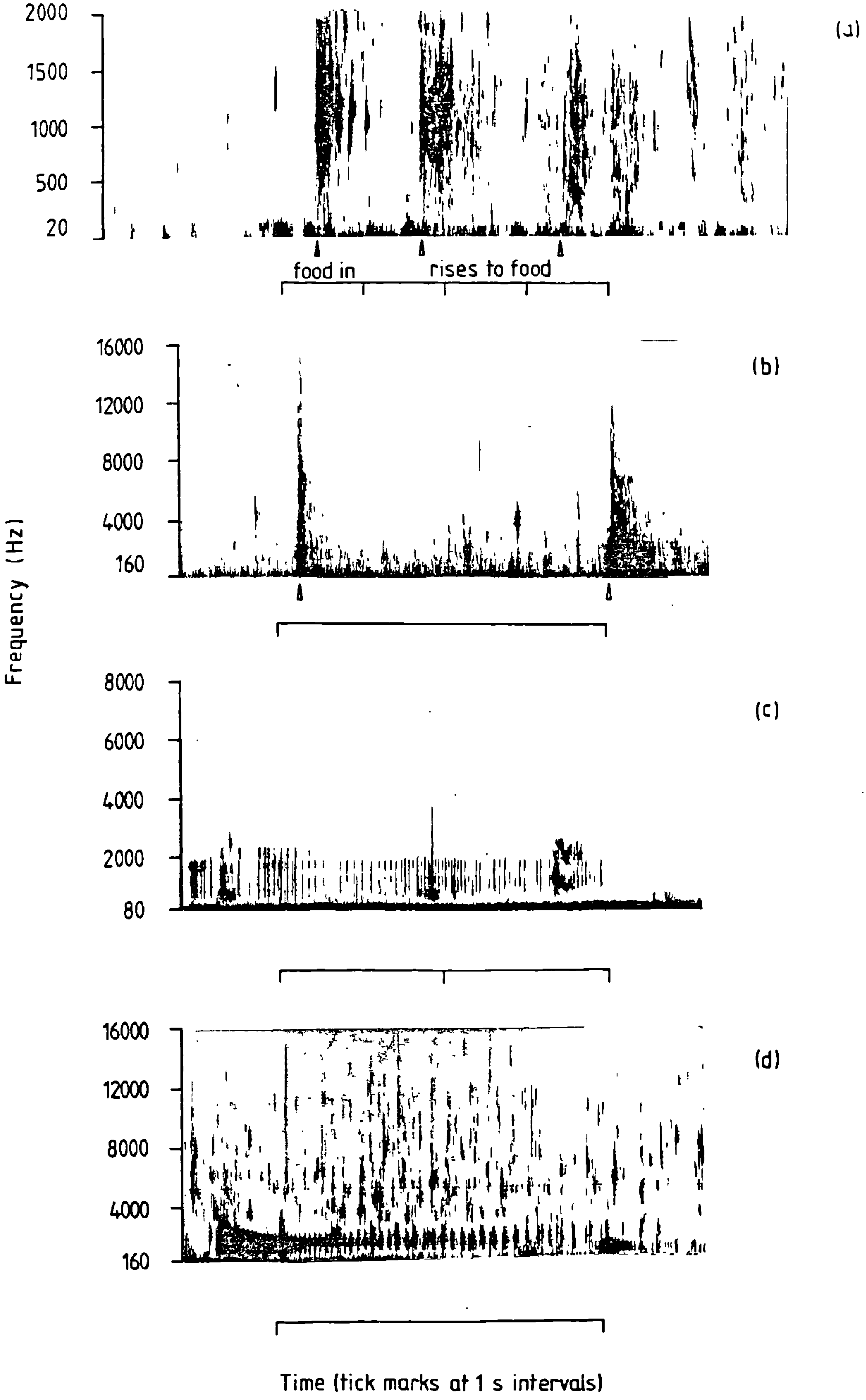
Broad band levels (20-25,000 Hz) 1 m from feeding rises reached a maximum of + 22 dB// 1μbar. To predict whether rainbow trout are capable of hearing these feeding noises this level has to be converted into the sound pressure, measured with a filter with a width similar to that of their frequency range (Hawkins and Johnstone, 1978). This level was calculated by summing the spectrum levels of the noise (Figure 4.2), obtained using octave filters, over the bandwidth 30 - 380 Hz. The calculation gave a maximum sound pressure level for the feeding noises of + 15.5 dB// 1μbar and is a maximum level because auditory sensitivity is not constant throughout the range 30 - 380 Hz, but

Figure 4.1. Sonograms of the noises associated with feeding rainbow trout (~500 g) showing changes in amplitude and frequency structure with time.

(a) shows food striking the water (arrow) and the response of two rainbow trout (arrows) to the floating food.

(b) shows the "clicks" associated with mastication

(c) and (d) show two post-feeding noises, possibly associated with the movement of air within the fish.


2000
1500
1000
500
20
(a)
food in
rises to food
16000
12000
8000
4000
160
(b)
8000
6000
4000
2000
80
(c)
16000
12000
8000
4000
160
(d)
Frequency (Hz)
Time (tick marks at 1 s intervals)

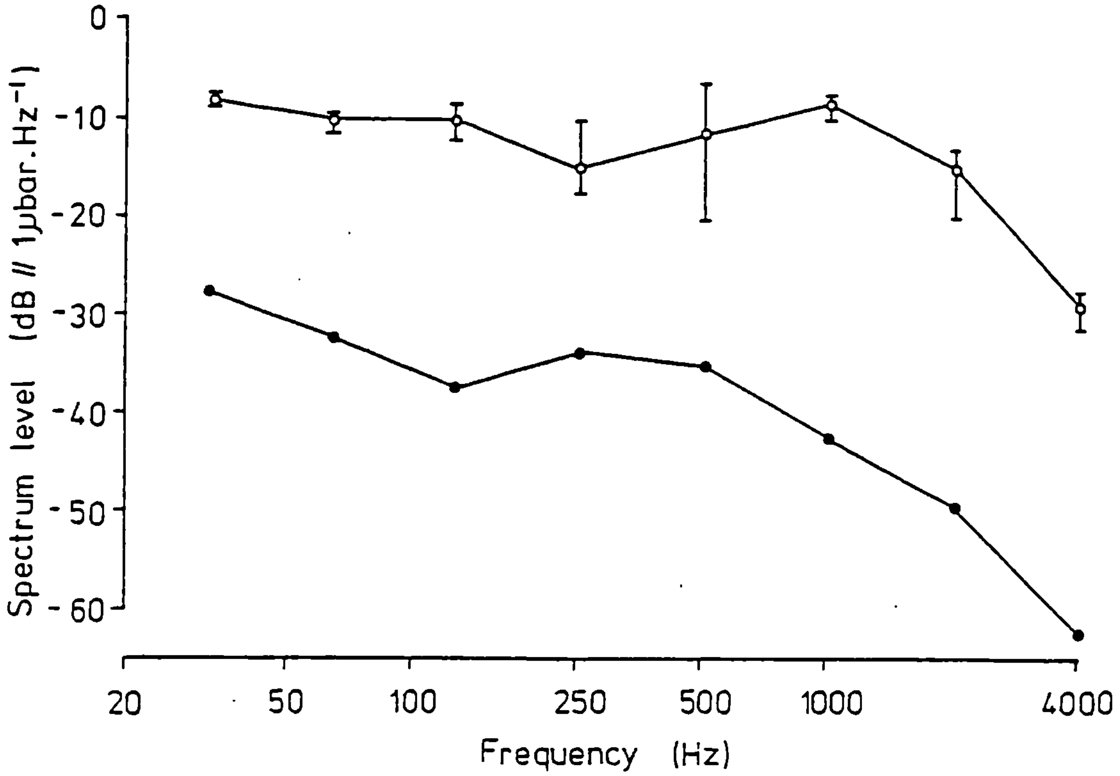


Figure 4.2. A spectral-analysis of the noise of rainbow trout feeding at the surface. Measurements taken approximately 1 m from the rises with the hydrophone at a depth of 1 m. Graph shows the mean (± range) of the levels from four fish (o) and, for comparison, the ambient noise at sea state 0 (●) in Dunstaffnage Bay.

decreases towards the edge of the range. To determine whether the rainbow trout are capable of hearing the sound, this level can be compared with the threshold of 0 dB// 1μbar at 140 Hz (Section 2.3.2.5.). The fish would therefore certainly hear the sound at 1 m and if one assumes spherical spreading which, although not strictly applicable to transient noises, is probably a reasonable approximation for these conditions (Section 2.3.3.), for up to 5m from the source. The noise may even be audible over larger distances because, in Atlantic salmon at least, the thresholds for noises generated in shallow water, or near the surface, extend below 0 dB// 1μbar (Hawkins and Johnstone, 1978).

Food pellets striking the water made similar, although less intense low frequency noises. Band levels of up to + 10.8 dB// 1μbar were recorded with the theoretical 30 - 380 Hz filter. Therefore, these noises would again be audible at 1 m and, with spherical spreading, approximately 3 m or more from the source.

Atlantic salmon were generally less voracious feeders than rainbow trout, although this depended on their motivation to feed, and therefore produced less intense noises than the rainbow trout. Smaller (50 g) rainbow trout produced less intense noises than larger fish so their propagation would also be more limited.

In addition, "clicking" and "scraping" type noises were heard when fish took food pellets into their mouths and these were particularly audible during feeding on sinking pellets when they were not masked by splashing noises. These noises were of a relatively short duration (Figure 4.1b) with most energy below 8,000 Hz, although components were observed up to 16,000 Hz. Broad band (25 - 25,000 Hz) levels extended up to + 13.6 dB// 1μbar although with the theoretical 30 - 380 Hz filter their level only reached + 7.74 dB// 1μbar. Therefore, this noise would probably be audible at only a few metres from the source. Similar stridulatory noises have also been recorded from a variety of species (Winn, 1964; Tavolga, 1977) and are caused by the action of the teeth against the food.

After feeding, several "rumbling" or "croaking" type noises were heard. Two sonograms of such sounds are shown in Figures 4.1c and 4.1d. These were of a variable duration and were composed of individual pulses with a variable time interval between them. The noise shown in Figure 4.1d had a broad band level of + 8 dB// 1µbar and was undetectable from background noise below 500 Hz. That illustrated in Figure 4.1c had a broad band level of + 16 dB// 1µbar and a theoretical filter level of + 8.55 dB// 1µbar. The levels of the two noises probably vary because the unknown fish making these noises were at different distances from the hydrophone. Both noises had a fundamental frequency around 1000 Hz and therefore most of the noise would be inaudible to other salmonids. Where the frequency extends to below 500 Hz the sound may be audible over only a few metres. Similar "rumbling" type noises have also been recorded by Neproshin (1972) and Neproshin and Kulikova (1975) and the latter authors suggest they are due to the movement of air within the fish, either through the pneumatic duct or the gut.

4.3.2. Response to feeding noises

No reactions to the feeding sounds were recorded during several playback experiments at both normal and +10 dB higher levels. The previous section suggested that rainbow trout should hear these noises for several metres and experiments were only carried out under calm conditions to minimize the risk of masking by ambient noise.

The above result may have been a result of the artificial stimulation of noise transmitted from a tape recorder and loudspeaker. In order to eliminate this possibility, and investigate whether feeding noises were attractive under 'natural' conditions, a different approach was taken. This approach involved blocking out external visual stimuli from a 2 m x 2 m x 2 m net by covering each of the four side panels with black polythene sheeting which, as demonstrated in Section 2.2.2., is acoustically transparent at 140 Hz. Fifty, 50 g rainbow trout were placed in this cage. Two similar sized nets, one containing fifty, 500 g and the other one hundred, 50 g rainbow trout, were placed on two sides of the experimental net 0.5 m away. Underwater television was then used to monitor the response of fish in the unfed experimental cage to acoustic cues emanating from feeding fish in the adjacent nets.

No stimulation was observed during these experiments, although if the sheeting was removed the fish in the unfed cage were strongly excited and attracted towards the visual stimuli of individuals feeding in the adjacent nets.

4.4. DISCUSSION

The sounds recorded during the present study can be divided into three main categories; hydrodynamic, stridulatory and those associated with a movement of air within the fish. All were probably produced involuntarily in both S. gairdneri and S. salar and there was no evidence for any active sound production as suggested by Neproshin (1972) and Neproshin and Kulikova (1975) in some spawning salmonids.

Hydrodynamic sounds are produced by the motion of fish through the water (Tavolga, 1977), but were only recorded when the fish broke the water surface, not when they were below it, as described for some other species by Moulton (1960) and Protasov (1965). Neproshin and Kulikova (1975) also failed to record such noises. Sounds would, however, be produced during swimming but be too low a frequency to be recorded with normal recording equipment. The maximum frequency produced depends on the maximum tail beat frequency which is inversely related to fish length and depends on the contraction time of the lateral muscles (Wardle, 1977). The maximum tail beat frequency (F, Hz) can be calculated from the fish length (L, m) according to the equation:

$F = 10\,L^{-0.4}$ (Batty, in Denton et al., 1979)

Thus, salmonids between 0.15 and 0.40 m in length can produce sounds with a maximum frequency of 21 and 14 Hz respectively during swimming. Even so, these sounds were apparently not effective stimulants at distances greater than approximately 0.5 -1.0 m.

Hawkins and Johnstone (1978) found that the auditory sensitivity in Atlantic salmon decreased down to 32 Hz although Weber and Schiewe (1976) recorded lateral line microphonics in rainbow trout in response to frequencies of several Hertz. Pitcher et al. (1976) found that blinded saithe, Pollachius virens, were only able to respond to schooling colleagues, via the lateral line, within a distance of one body length and Sand (1981) also suggested that the trunk lateral line was only stimulated over relatively short distances. Thus, although fish may respond to such acoustic stimulation, which indeed is important in normal shoaling behaviour (Pitcher et al., 1976; Pitcher, 1979; Partridge and Pitcher, 1980; Partridge, 1981), it may not be effective at the minimum distance employed (0.5 - 1.0 m) in the present study. These results do not imply that these low frequency stimuli are not an important sensory input in mediating more intimate intraspecific behaviour in rainbow trout although more precise quantitative experiments (e.g. Pitcher, 1979) would be needed to verify this.

Neproshin (1972) and Neproshin and Kulikova (1975) recorded non-feeding stridulatory sounds from a variety of salmonids up to a broad band level (frequency unknown) of + 31 dB// 1μbar. Again, a large part of this signal would have been inaudible because of its wide frequency range. Protasov (1965) describes a variety of such feeding noises and also illustrates how they vary with the type of food being eaten.

The exact source of the "rumbling" type sounds is unknown, but the possible mechanisms involved are described by Neproshin and Kulikova (1975) and are probably a result of a movement of air within the pneumatic duct or gut. Production is therefore likely to be enhanced after an excursion to the surface to feed. Stober (1969) also recorded similar sounds after cutthroat trout (Salmo clarki) rose to the surface. Neproshin (1972) also recorded some drumming sounds up to levels of + 38 dB// 1µbar during spawning and Neproshin and Kulikova (1975) have suggested this may be due to the stimulation of muscles overlying the swimbladder at its anal end. No such sounds were recorded during the present study.

The loudest signals, and hence those that would propagate furthest were recorded during "rising" for food. Neproshin and Kulikova (1975) measured broad band levels of up to + 31 dB// 1µbar at 1 m from the fish although the details of depth of the hydrophone or the filter used are unknown. Similarly, Maniwa et al. (1973) reported that the "swimming and bait eating" sounds of pink salmon reached a broad band level of + 37 dB// 1µbar centred at 200 Hz although no further details of the recording conditions were given. The broad band (20-25,000 Hz) levels recorded in the present study reached + 22 dB// 1µbar and it is possible that the hydrophone was further away from the fish than in the latter study. It was, however, difficult to avoid knocking the hydrophone and hence introducing low frequency noise if it was placed closer to the source. The hydrophone may also have been deeper than other studies although at 1 m it would give an indication of the propagation of the noise, particularly as the surface wave is rapidly dissipated.

The lack of reaction to artificially generated feeding noise in the playback experiments suggests that rainbow trout cannot be controlled in this way. As they appeared to be theoretically capable of hearing the stimulus, it is perhaps surprising that there was no reaction. One of the reasons may have been that the components of the splashing noises that were audible were similar to the ambient noise in Dunstaffnage Bay and they were, therefore, not sufficiently different to act as a conditioning stimulus. The transient nature of the stimuli may also have decreased the ability to detect the component stimuli as Hawkins and Horner (after Hawkins, 1981), for example, showed that shorter sound stimuli require higher amplitudes for their detection by the cod, Gadus morhua. Additionally, the rainbow trout may have been aware of the feeding sounds but required a visual stimulus as a releaser. If this was the case, then it is further evidence for the importance of visual stimulation in salmonid feeding behaviour.

SECTION 5

GENERAL DISCUSSION AND SOME PRACTICAL IMPLICATIONS

The experiments in Dunstaffnage Bay (Section 2) showed that rainbow trout were relatively easily conditioned in a cage suggesting that there is a potential for controlling the movements of "free-ranging" fish using sound. In addition, the ability of ultrasonically tagged rainbow trout to move up to 150 m in response to other feeding cues (Section 3) suggests that, given a loud enough signal, they may, perhaps be controlled over such distances. Despite the negative results obtained during the field experiments described in Section 3 (which were probably due to the adverse experimental conditions but were also confounded by the importance of visual cues, the poor auditory capability of rainbow trout and the low signal amplitude), the technique may therefore be useful for a precise control of fish behaviour. It might, for example, be used for leading rainbow trout to a harvesting point in a suitable location.

The best waters for using this technique would be deep with a hard bottom so that less signal would be lost by bottom absorption. The conditioning technique should be chosen with due regard to its application. For purely feeding, several transducers, placed as deep as possible to avoid undue surface loss, could be used in appropriate positions to signal feeding at one or more feeding stations; Section 2.3.2. showed that rainbow trout were capable of learning such a task by using purely visual cues to locate the feeding station. To 'herd' fish to a harvesting point, on the other hand, conditioning should aim to minimize the importance of visual cues by 1) introducing conditioning near to harvesting time, 2) placing the loudspeaker close to the feeding point and 3) using two or more feeding stations and randomly alternating the trials between them in a manner similar to Olsen's training experiments with saithe (Olsen, 1976). Conditioning would be best introduced at times of high feeding motivation and the end of the summer is probably the most convenient time because it satisfies this requirement and is also the end of the main growing season. By leading fish around a water more fish could be attracted because of the mutual stimulation of activity between individuals.

Using the sound as a signal to feed requires only that the fish are able to hear the conditioned stimulus and this criterion is easily obtained. Leading fish to harvesting points, however, requires some directional hearing sense and therefore needs more experimentation. This work should aim to quantify the threshold for hearing and any directional sense in terms of the three dimensional particle displacement and sound pressure amplitudes. Knowledge of these crucial thresholds could then be used to determine the ability of rainbow trout to be controlled in any given sound field.

The disadvantages of using sound as a controlling stimuli is that relatively sophisticated and expensive equipment is required to produce sufficiently loud low frequency signals (Tavolga, 1980). Simple manipulation of feeding points does not and also shows considerable promise for controlling the movements of rainbow trout.

Supplementary feeding points were shown to be the controllers of at least the summertime (April - September) movements of fish in Loch Charn. In Loch Fad the accidental introduction of waste food also had a significant effect on the distribution of rainbow trout. This distribution, after April at least, was found to be analogous to that of a natural brown trout population in Loch Leven (Thorpe, 1974a) with the larger fish aggregating at the prime feeding sites, although it was converse to it in terms of the spatial location of the stocks. Supplementary feeding points may, therefore, be used deliberately to control the movements of rainbow trout for extensive fish farming.

Rainbow trout are a good species to use for any "free-range" farming enterprise because of their opportunistic feeding behaviour and relatively wide ranging movements which allows them to consume a wide variety of available natural food and means they can be attracted, in the long term at least, over distances of up to 2 km. This distance is considerably greater than the area that could be covered by a sound signal. This mobility, however, may also be a problem because, as Brown (1970) suggests, rainbow trout introduced into lakes are particularly susceptible to loss through any feeder streams or outflows.

The attraction of fish to the cages in Loch Fad showed that escapees from a fish farm could be used as an extra source of production. These fish may provide an extra source of income for the fish farmer and, because they consume waste food which would otherwise accumulate on the bottom, are useful pollution controllers. In fact, they probably regulate their numbers in relation to the amount of available waste food and judicious cropping of these fish could ensure an influx of fish to the cages (i.e. a maximum harvest) and remove some of the nutrients released from the farm into the loch and may therefore help to reduce the rate of eutrophication (Beveridge, 1980). Alternatively, with the correct manipulation of both the method and level of feeding, rainbow trout may be deliberately farmed in waters at least as big as Loch Fad.

Deliberate farming should aim to ensure optimal use of natural food during the on-growing period as supplementary food is the single most expensive item in intensive fish culture (Landless, 1974b). This situation could be achieved by correct stocking and feeding levels and in oligotrophic waters by feeding over as wide an area as possible. This technique should stimulate predation on natural food and reduce the hierarchical effect around a point food source by alllowing all fish easy access to food even though some aggregation would be desirable in order to minimize food wastage. It would be absolutely essential, however, to use floating food for this latter reason. Use of floating food would also allow feeding activity to be easily monitored. In more productive waters simply reducing the feeding level might promote wider ranging movements and good use of natural food. However, more experimentation is required to determine correct stocking and feeding levels and techniques in relation to natural food consumption, although the observed behaviour will probably be predictable in terms of a cost/benefit energetic type model (e.g. Rubenstein, 1981).

Growth and survival were good throughout the summer period (April - September) although more extensive data is required to determine the optimum return. For example, the survival of smaller fish would be less, particularly if they overwinter (Cragg-Hine, 1975), but this loss may be offset, to an unknown degree, by the cheaper cost of their production.

Fish may be harvested by increasing feeding levels at point food sources, perhaps in a suitable netting location. At this time the hierarchical effect could be used to some advantage because the larger, better conditioned fish would probably be captured first. Removing the larger fish would then allow smaller ones into the feeding area for subsequent capture. In addition, particularly in oligotrophic waters, the large fish may be easier to catch because natural production would be less likely to fulfill their feeding requirements. Again, late summer would probably be the best time to harvest the fish because it is the end of the growing season and feeding motivation is still high. Later in the year feeding motivation declines (Section 2; Wankowski, 1981) and harvesting may be less successful, although more experimentation on the annual variation in the degree of aggregation is required.

On a smaller scale for the purpose of a sport fishery, supplementary feeding could be useful for reducing mortalities resulting from inter- and intra-specific competition for food in overstocked waters (Miller, 1958). A feeding area where angling is forbidden could also be used to keep a pool of fish, some, or all, of which may be released for angling by reducing or stopping supplementary feeding. This technique could be an alternative policy to constant restocking throughout the season which is the normal management procedure (Cresswell and Williams, 1979). It would, however, allow fish to be grown relatively cheaply and enable them to become familiar with natural food. The economic validity of such techniques require further investigation.

In summary, there is some potential for the control of the movements of rainbow trout, and probably other species, using sound although the behaviour of rainbow trout makes them a very amenable subject for a simple control system using supplementary feeding points.

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APPENDIX A

SOME OBSERVATIONS OF THE BEHAVIOUR OF RAINBOW TROUT IN SEA CAGES

A.1. INTRODUCTION

The behaviour of salmonids in cages has received scant attention in the literature. Sutterlin et al. (1979) have published a series of observations of the behaviour of Atlantic Salmon (S. salar), rainbow trout (S. gairdneri) and pink salmon (Oncorhynchus gorbuscha) held in fish pens on several Norwegian fish farms. Atlantic Salmon were found swimming in a consistent anticlockwise or clockwise direction around the pen and this pattern of behaviour did not change with the tide, season or age of the fish. Their data concerning rainbow trout were more limited and no consistent swimming pattern was demonstrated although the authors concluded that, because this species was conditioned to expect food from humans, any consistent swimming pattern was probably disrupted when observers were present on the cage. Using similar direct observation techniques, Wilton (1980) recorded some circular activity in groups of rainbow trout on two out of three freshwater cage farms although again he could have inadvertently excited these fish by his presence.

In the present study observations were made on the behaviour of undisturbed rainbow trout in sea cages moored in Dunstaffnage Bay using a remotely operated underwater television system. The aim of this appendix is to describe some of this behaviour.

A.2. MATERIALS AND METHODS

All the information discussed below is based on recordings made on video tape for 1 min prior to the conditioning trials described in Section 2.3.1. All details of instrumentation and the experimental animals and situation are given in Section 2.2. Observations were made from July 1979 until April 1980 on groups of 50 rainbow trout in 3.5 m x 3.5 m x 3.5 m nets. Most of the information reported below, however, was derived from different groups of fish originating from the same stock and held during September 1979 (T = 13°C) and March 1980 (T = 7°C). The mean fork length (± 1 s.d.) of the fish used during these periods was 232 mm (± 12) and 310 mm (±13) in September and March respectively.

A.3. RESULTS

A.3.1. Depth distribution of caged rainbow trout

The aim of this section was to quantify the vertical distribution of fish within the sea cages in Dunstaffnage Bay. This was done in two stages by:

(1) Calibrating the television camera and monitor screen by hanging an object of known size at a known depth within the cage and measuring its size on the video monitor.

(2) Taking the mean total length of fish within the cage, measuring the length of individuals on the video monitor and then assigning them to a certain depth by applying a correction calculated from (1).

During analysis care had to be taken to ensure constant contrast and brightness levels on the monitor controls. To minimize distortion, data were only considered within a 1- m square surface area water column centered in the middle of the cage and video monitor. The camera calibration yielded the following significant regression:

$$D = 3.0298 - 0.1975 \frac{R}{A}$$

where D = depth (m)

R = real size of object

A = apparent size of object on video screen

$t = 27.90$; d.f. = 22; $p < 0.001$

This regression allowed the depth of individual rainbow trout to be back calculated according to their size on the video monitor.

Data was obtained from two experiments, one in September 1979 (6 days data) and one in March 1980 (3 days data). Both clear and overcast days were included in the two sampling periods. The results are shown in Figure A.1. Taking the 95% confidence limits of the mean total lengths and regression into account the 95% confidence limits of a depth estimate of 0.25 m were 0.25 ± 0.23 m in both September and March.

The results (Figure A.1) show that in both cases the fish were aggregated close to the surface. Both distributions were tested against the expected distribution that they were evenly distributed within the top 2.0 m of the water column using χ^2. The difference from the expected distribution was significant at the 0.1% level in both cases (September; $\chi^2 = 598.07$; d.f. = 7; $p < 0.001$; March; $\chi^2 = 109.36$; d.f. = 7; $p < 0.001$). They were also significantly different from each other ($\chi^2 = 78.58$; d.f. = 7; $p < 0.001$) showing that in September fish aggregated nearer the surface.

Although the movement of the rainbow trout during undisturbed behaviour was restricted to the surface layers they made use of the deeper and darker portions of the net when frightened.

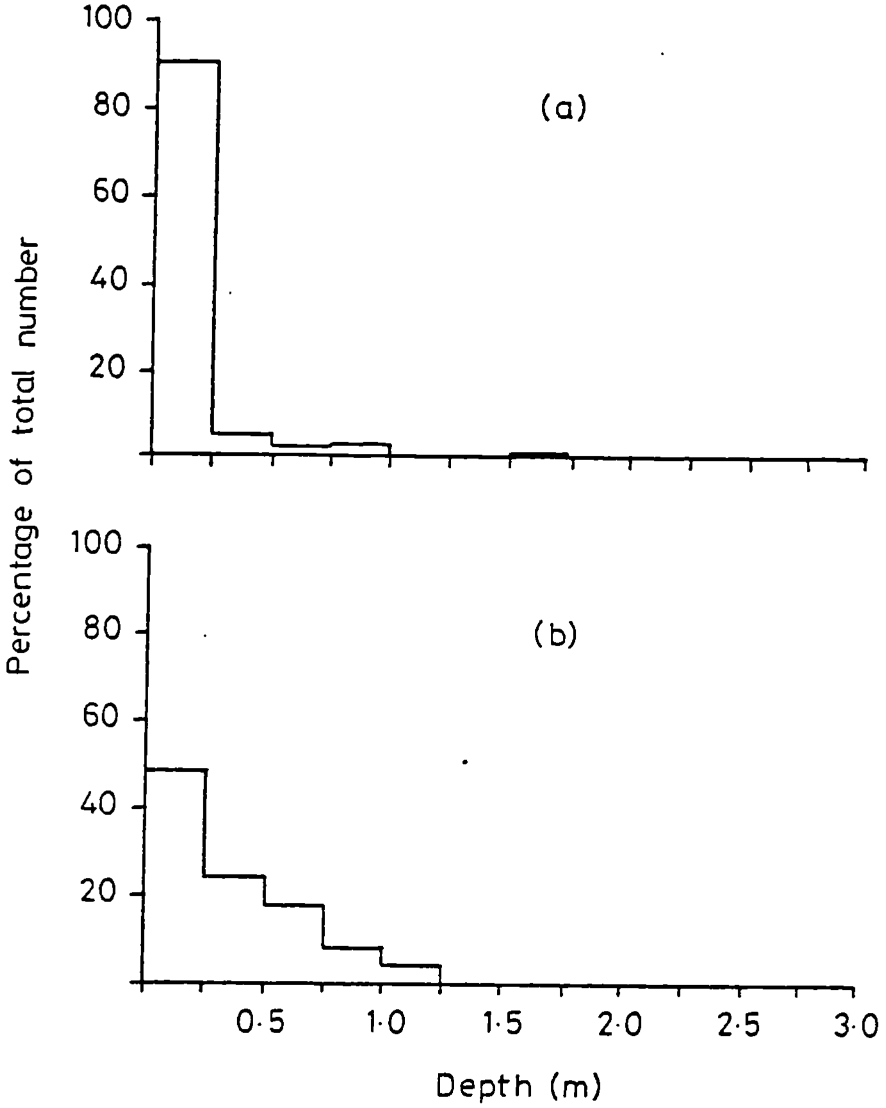


Figure A.1. Depth distribution of groups of 50 caged rainbow trout.

(a) September, 1979; mean total length, 240 mm (s.d. = ± 11); 108 observations

(b) March, 1980; mean total length, 317 mm (s.d. = ± 14); 75 observations

A.3.2. Swimming behaviour of caged rainbow trout

The horizontal distribution of rainbow trout within the cage was related to both the velocity and direction of the water current flowing through the cage. Although interpretation of these responses is difficult without concurrent measurements of tidal flow the aim of this section was to illustrate some of the gross features of these responses. These responses were related to some tidal flow data obtained over three days during September, 1974 which show the approximate duration of slack water with respect to the tidal regime (Edwards, pers. comm.). These periods must, however, be taken as approximate values because they vary considerably (e.g. range of the duration of the slack water period after low tide = 1.31 - 19.7 min; n = 6 : range of the start of this period after low tide = 1.81 - 2.96 h; n = 6). Consecutive current measurements would therefore be required to describe a quantitative relationship between current velocity and swimming behaviour.

Two main types of distribution were observed within the cage:

(1) Higher water velocity behaviour when fish were aggregated in a school type structure and maintained station against the current (Figure A.2 a,c).

(2) Low velocity or slack water behaviour when individuals were more randomly distributed within the cage and there was no preferred direction of orientation (Figure A.2 b,d).

Between these two extreme types of behaviour, varying degrees of aggregation were observed. The thresholds for any of the responses could not be predicted from the tidal flow data because these measurements were not taken concurrently. In Dunstaffnage Bay, however, fish were observed holding station near the surface in current velocities which were probably up to $25cm.s^{-1}$.

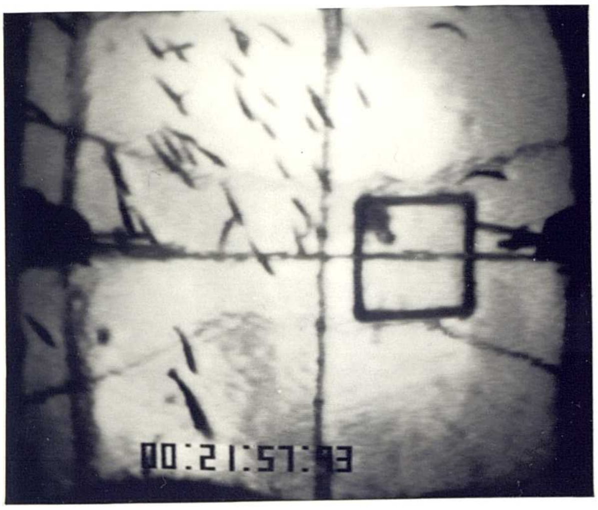
Figure A.2. Rainbow trout in the sea cage in Dunstaffnage Bay showing variations in the polarity and aggregation with tidal flow Photographs taken from video tape.

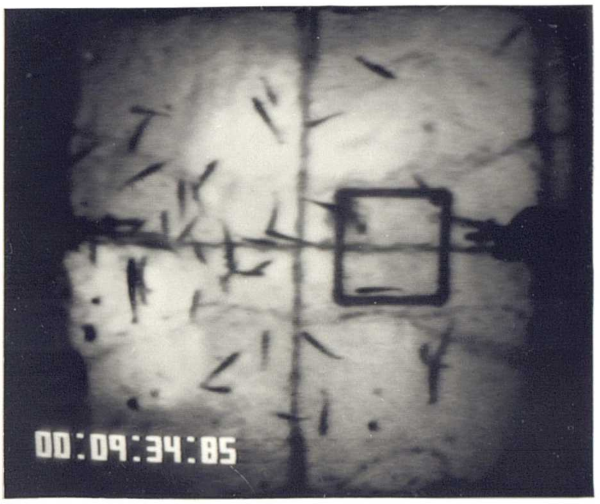
(a) September : current flowing through cage

(b) September : slack water

(c) March : current flowing through cage

(d) March : slack water


a
00:21:57:93


b
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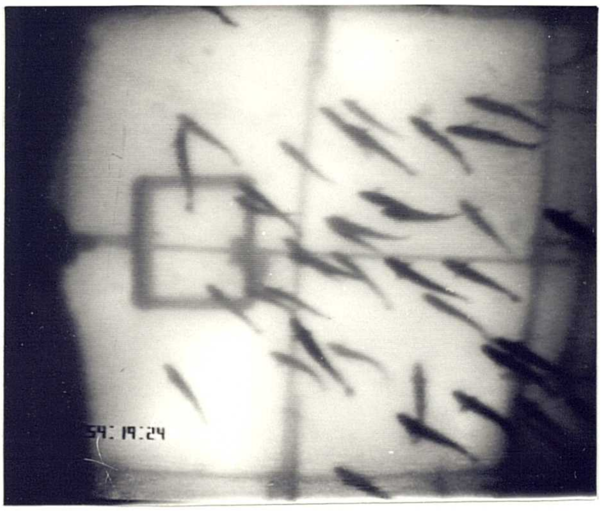
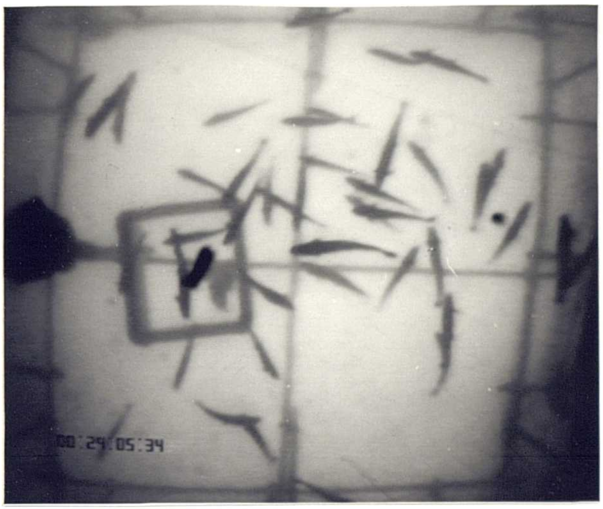

c
54:19:24


d
00:29:05:34

When a group of fish appeared to be maintaining their position in the current, observations over periods of up to 20 min showed that individuals changed position in the shoal and would drift with the tide and then readjust their position, sometimes to another part of the group. This type of behaviour appeared more prevalent at lower current velocity. In addition, not all individuals were involved in the shoal to the same degree because a small number of individuals were usually seen in other parts of the cage. Whether or not these fish were the same individuals is unknown. No consistent pattern of orientation as described by Sutterlin et al. (1979) for Atlantic salmon was ever seen in rainbow trout.

Although during September a constant feature of their behaviour was that fish were inactive unless forced to swim against the tide or were disturbed, observations during March revealed a different pattern of slack water swimming behaviour. Behaviour at higher current velocities was similar at all times. During slack water in March the rainbow trout swam in a circular anticlockwise manner in a similar way to the Atlantic Salmon of Sutterlin et al. (1979). To illustrate this behaviour the video tapes were analysed in the following manner:

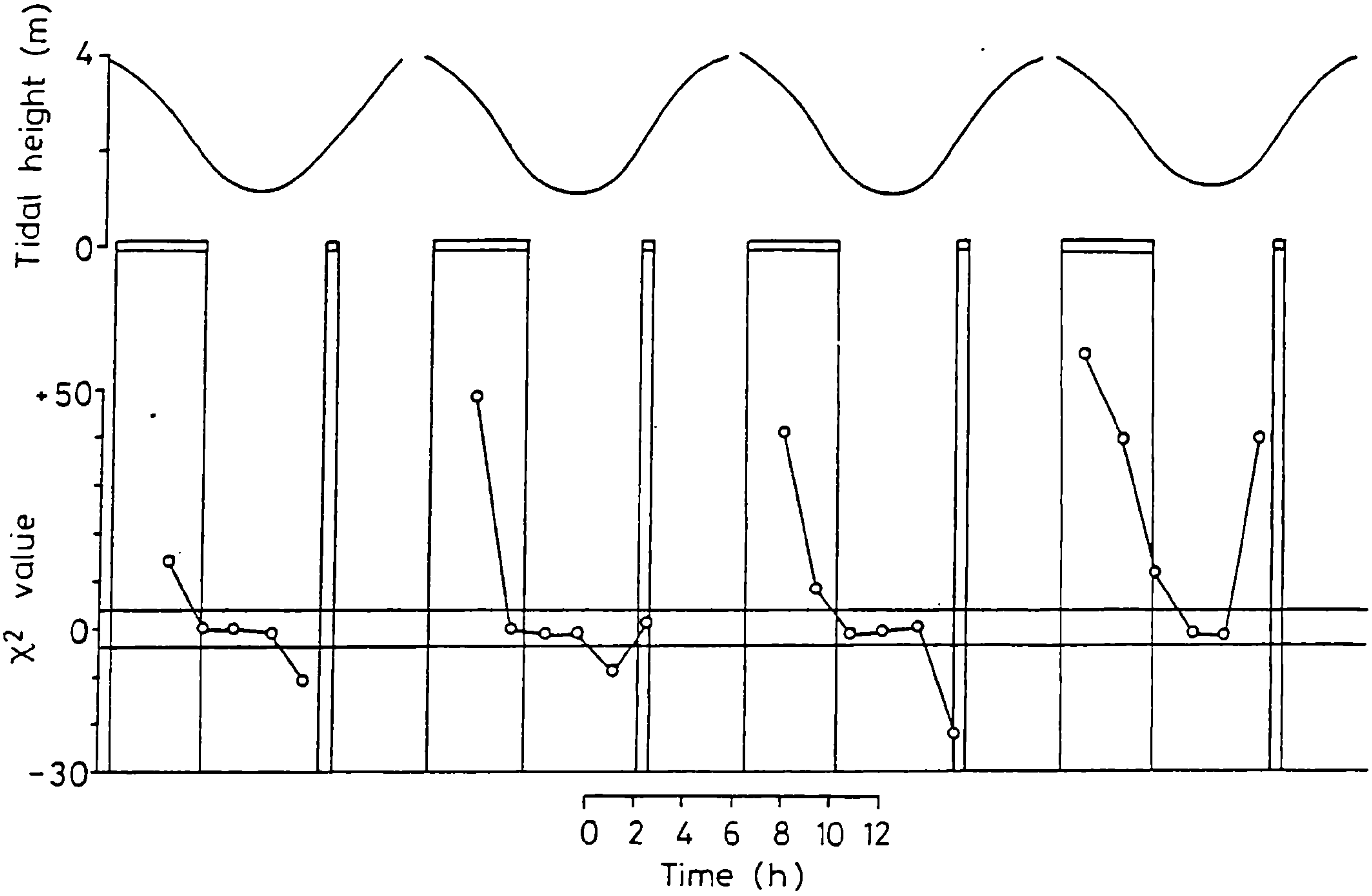
(1) The cage was divided into four equal triangular sectors and the total number moving across each sector boundary in each direction was counted for 1 min before each trial.

(2) The null hypothesis of equal numbers moving in anticlockwise and clockwise directions was tested by comparing the observed distribution with that predicted by the null hypothesis using a χ^2 test (with Yates correction).

Figure A.3 illustrates this change in behaviour with the tidal cycle and the mean time and duration of slack water predicted from the three days data taken during September 1974. This figure shows how anticlockwise swimming

Figure A.3. The relationship between the swimming behaviour of caged rainbow trout and the tidal cycle over four consecutive days during March 1980.

The bars below the tidal height curves represent the mean periods of slack water predicted from three days data from September 1974. The tidal height shown is the height above Chart Datum. Positive and negative χ^2 values represent net anticlockwise and clockwise movement respectively. The horizontal lines on the χ^2 graph show the 5% significance levels for χ^2 with one degree of freedom ($\chi^2 = 3.84$).


Tidal height (m)
4
0
+50
χ² value
0
-30
0 2 4 6 8 10 12
Time (h)

behaviour is correlated with the predicted slack water which, in Dunstaffnage Bay at least, occurred between high and low tide. There was also some significant clockwise motion after low tide which occurred when there was a shoal in a favoured corner of the cage and there was a significant movement of individuals from the front of the shoal, around the cage, to the rear of the shoal. This type of behaviour was typical of intermediate flow velocities and showed how the direction of the water current could stimulate circular activity in a particular direction.

The development of this March behaviour was not observed. Video tapes of a group of the same stock of fish taken during January failed to show this circular activity.

A.4. DISCUSSION

The finding that fish were aggregated close to the surface and not randomly distributed in depth throughout the cage shows that the deeper parts of the cage are under-utilized and measurements of physical variables taken at these depths (e.g. Landless and Edwards, 1976) may not be relevant to the majority of fish within the cage. Wilton (1980) also found that rainbow trout (< 250 g) congregated near the surface on some freshwater cage farms. The deeper parts may, however, be used during stressfull periods such as rough weather and video observations showed that rainbow trout, frightened by birds or humans, fled to the deeper portion of the cage. They may also use these deeper parts at night (Wilton, 1980).

There may be several reasons why the rainbow trout preferred to remain near the surface. Feeding floating food may have biased the distribution towards the surface as Ringler (1979) showed that drift feeding brown trout, Salmo trutta, altered the depth searched in response to the local abundance of prey. They may also have prefered the temperature of the water near the surface, although the response would probably vary with the actual temperature, the other available temperatures and other environmental parameters. Low surface salinities could also have attracted fish to the surface. The distribution of rainbow trout observed in this study appears to contradict the results of Kwain and McCauley (1978) who found that yearling rainbow trout are negatively phototactic under artificial illumination and DeVore and White (1978), who showed that brown trout prefer cover where available. The horizontal distribution studies of the rainbow trout in the conditioning experiments (Section 2.3.1.2.3.), however, suggests that they may show some preference for shade, although recent evidence suggests that they may even be attracted to certain components of natural sunlight (Bullock, pers. comm.). Even so, it was obvious that a large number of fish were not in any significant shade and as they were aggregating near the surface such fish would be more likely to suffer from sunlight related dermatological problems (Bullock, pers. comm.).

A decrease in temperature (September, 13°C; March 7°C) as well as a variation in the aforementioned environmental variables could have been responsible for the differences between the behaviour in September and March. The differences in size could also have affected the distribution as Wilton (1980) suggested that larger rainbow trout usually remained deeper in a freshwater cage than the smaller (< 250 g) fish. There may also be a seasonal variation in the response and, therefore, seasonal observations, with simultaneous current, temperature, salinity and ambient light measurements are required to determine the controlling stimuli of the observed behaviour.

The contrast between the behaviour of the rainbow trout in this study and Sutterlin et al's Atlantic salmon may be a real reflection of the difference in behaviour between the two species or a result of site specific behaviour in

Dunstaffnage Bay. Wilton (1980), using direct observation, found that circular activity was present on two out of three freshwater cage farms and, therefore, there may be some variation between sites. The smaller groups of fish used during the present study could also have depressed activity because larger groups may be more active as a result of social facilitation. More observations are obviously needed on several sites, although if there is a real difference between the two species it may be a reflection of the differences in their migratory behaviour, Atlantic salmon being a greater migrant than the cultured rainbow trout. The circular activity that did develop in the rainbow trout could be an expression of this migratory instinct. Seasonal changes in the physiological response of freshwater rainbow trout to seawater transfer have been detected by Jackson (1979) who suggested this was an expression of the partly migratory ancestry (in the steelhead trout form) of the domesticated rainbow trout. The appearance of a circular swimming behaviour may also be a reflection of this migratory ancestory.

Changes in size as well as environmental variables may have stimulated the activity in March even though one would have expected activity to be less at the lower March water temperatures (Hergenrader and Hasler, 1967). Activity may be stimulated during spring, however, because Holliday _et al._ (1974) showed that the activity of wild brown trout is at an annual maximum during March and April when the freshwater temperature rises to 7°C.

The direction of circular activity was shown to be controlled by the tide and, with the small groups used, would also have been affected by the preferred position of fish within the cage. Herbert (1963) has also shown how currents stimulate circular "slack water" motion although Sutterlin _et al._ (1979) suggested that the variation in orientation between different stocks of Atlantic salmon could be genetically determined.

Shoaling is a well documented phenomena in the sea-going phase of S. gairdneri (in the steelhead trout form) and other salmonids (Hoar, 1976) and it was therefore not surprising to observe similar behaviour in sea-caged rainbow trout. Variation in schooling and shoaling tendencies with current velocity have also been recorded in a variety of species (Keenleyside, 1979). Kalleberg (1958) induced shoaling in young stream salmonids by stopping the current but there is no evidence for a change in the opposite direction in the marine stages of sea going salmonids. The increased polarisation of the shoal at higher current velocities has, however, been recorded in other marine species (Keenleyside, 1979).

If rainbow trout maintain station at higher current velocities then the hydrography of a cage site could have a direct effect on the exercise of this species. Kuipers (in Anon, 1982) found that exercised Atlantic salmon generally had a higher growth rate than resting fish that were fed the same rations. Thus, if the results observed in Dunstaffnage Bay are generally applicable the hydrography of a site may be correlated (within limits) with the growth of fish within the cages at that site.

APPENDIX B

DETAILED ANALYSIS OF THE DIET OF RAINBOW TROUT

B.1. LOCH CHARN

Breakdown of the animal component of the diet of Loch Charn rainbow trout expressed in terms of the actual and percentage of the total numbers and occurrence. Numbers in parentheses represent the percent number and occurrence of particular orders.

* indicates animals of terrestrial origin (terrestrial larvae) as given by Chinery (1979)

CLASS INSECTA	Number (n = 414)		Occurrence (n = 64)	
	Actual	%	Actual	%
Order Diptera		(44.44)		(35.94)
Sub-order Nematocera				
Unidentified Nematocera	1	0.24	1	1.56
Family Tipulidae				
Unidentified adult	1	0.24	1	1.56
Family Bibionidae				
Bibio sp.*	1	0.24	1	1.56
Bibio lanigerus or hybridus*	2	0.48	2	3.12
Bibio pomonae*	12	2.9	3	4.69
Dilophus febrilis*	4	0.97	2	3.12
Family Mycetophilidae				
Unidentified adult*	1	0.24	1	1.56
Family Ptychopteridae				
Unidentified adult	1	0.24	1	1.56
Family Simulidae (?)				
Unidentified adult	1	0.24	1	1.56

Family Chironomidae				
Chironomidae larva	9	2.17	6	9.84
pupa	117	28.3	26	42.62
Chironomus sp. adult	1	0.24	1	1.56
Sub-order Brachycera				
Family Empididae				
Hilara interstincta	1	0.24	1	1.56
Sub-order Cyclorrhapha				
Family Syrphidae				
Melanostoma mellinum	1	0.24	1	1.56
Unidentified Syrphidae	1	0.24	1	1.56
Family Scatophagidae				
Scatophaga stercoraria*	1	0.24	1	1.56
Family Sphaeroceridae				
Limosina sp.*	1	0.24	1	1.56
Family Muscidae				
Unidentified adult*	3	0.72	3	4.69
Unidentified Cylorrhapha	1	0.24	1	1.56
Unidentified Diptera adults	22	0.48	14	21.87
Unidentified Diptera pupa	2	0.48	1	1.56
Order Hymenoptera		(19.56)		(35.94)
Sub-order Apocrita				
Family Ichneumonidae				
Netelia virgatus*	1	0.24	1	1.56
Netelia latungulus*	1	0.24	1	1.56
Hydrophanes scabriculus*	1	0.24	1	1.56
Syrphoctonus flavolineatus*	1	0.24	1	1.56
Campoplex sp.*	1	0.24	1	1.56
Plectiscus sp.*	1	0.24	1	1.56
Unidentified Ichneumonidae*	3	0.72	3	4.69
Family Proctotrupidae				
Codrus longicornus*	1	0.24	1	1.56
Superfamily Chalcidoidea				
Unidentified adult*	1	0.24	1	1.56
Family Formicoidae				
Myrmica scabrinodis*	44	10.63	9	14.06
Myrmica ruginodis*	9	2.17	4	6.56
Formica lemani*	1	0.24	1	1.56
Formica fuscal*	1	0.24	1	1.56
Lasius flavus*	1	0.24	1	1.56
Lasius mixtus*	1	0.24	1	1.56
Unidentified Formicoidae*	2	0.48	2	3.12

Family Vespidae				
Vespula vulgaris*	1	0.24	1	1.56
Family Apidae				
Apis mellifera*	6	1.45	4	6.35
Unidentified Hymenoptera adults	4	0.67	4	6.55
Order Coleoptera		(6.76)		(29.68)
Sub-order Adephaga				
Family Carabidae				
Feronia madidus*	1	0.24	1	1.56
Unidentified Carabidae adult*	1	0.24	1	1.56
Family Dytiscidae				
Hydroporus discretus	1	0.24	1	1.56
Sub-order Polyphaga				
Family Hydrophilidae				
Sphaeridium scarabeoides	2	0.48	2	3.12
Family Staphylinidae				
Philonthus puella*	1	0.24	1	1.56
Mycetophorus splendens*	1	0.24	1	1.56
Unidentified Staphylinidae* adult	8	1.93	6	9.37
Family Geotrupidae				
Geotrupes stercocarius*	1	0.24	1	1.56
Family Coccinellidae				
Aphidecta obliturata*	3	0.72	3	4.69
Family Chrysomelidae				
Phylodecta vulgatissima*	1	0.24	1	1.56
Unidentified Chrysomelidae larvae	4	0.97	1	1.56
Unidentified Coleoptera adult	3	0.72	3	4.69
Unidentified Coleoptera larvae	1	0.24	1	1.56
Order Hemiptera				
Sub-order Heteroptera		(8.45)		(12.5)
Family Pentatomidae				
Pentatoma rufipes*	6	1.45	4	6.55

Family Miridae				
Psallus scholtzi*	1	0.24	1	1.56
Unidentified Heteroptera	2	0.48	2	3.12
Sub-order Homoptera				
Family Psyllidae				
Psylla alni*	1	0.24	1	1.56
Family Aphididae				
Unidentified Aphididae*	25	6.04	1	1.56
Order Ephemeroptera		(6.04)		(10.94)
Family Baetidae				
Cloeon (?) simile nymphal skin	11	2.67	44	6.55
Unidentified Ephemeroptera nymphal skins	10	2.41	7	11.47
Unidentified Ephemeroptera adult	4	0.97	2	3.12
Order Plecoptera		(1.45)		(7.81)
Family Nemouridae				
Nemoura cinerea	2	0.48	2	3.12
Unidentified Nemouridae adult	2	0.48	2	3.12
Unidentified Plecoptera adult	1	0.24	1	1.56
Unidentified Plecoptera nymph	1	0.24	1	1.56
Order Trichoptera				
Unidentified adult	4	0.97	4	6.25
Order Neuroptera		(0.72)		(4.68)
Family Hemerobiidae				
Unidentified adult*	2	0.48	2	3.12
Unidentified Neuroptera adult	1	0.24	1	1.56
Order Psocoptera				
Family Ectopsocidae				
Unidentified adult*	1	0.24	1	1.56
Order Lepidoptera				
Family Geometridae				
Unidentified larvae*	1	0.24	1	1.56
Unidentified insect larvae	19	4.59	15	23.44
Unidentified insect pupa	1	0.24	1	1.56

CLASS ARACHNIDA				
Order Araneida				
Unidentified terrestrial Araneida*	1	0.24	1	1.56
Order Acarina				
Sub-order Hydrachnellae		(3.38)		(10.94)
Family Mediopsidae	1	0.24	1	1.56
Family Hygrobatidae	2	0.48	2	3.12
Unidentified Hydrachnellae	11	2.66	5	7.81
CLASS CRUSTACEA				
Order Cladocera		(0.72)		(3.12)
Family Daphnidae				
Daphnia sp.	1	0.24	1	1.56
Unidentified Cladocera	2	0.48	1	1.56
CLASS GASTROPODA				
Order Basommatophora		(0.48)		(3.12)
Family Lymnaeidae				
Lymnaea peregra	1	0.24	1	1.56
Family Planorbidae				
Unidentified Planorbidae	1	0.24	1	1.56
Miscellaneous animal remains		(1.21)		
Unidentified animal remains (Insecta ?)	3	0.72	3	4.69
Feather	1	0.24	1	1.56
Terrestrial vertebrate faecal pellet	1	0.24	1	1.56

B.2 LOCH FAD

Breakdown of the animal component of the diet of Loch Fad rainbow trout expressed in terms of the actual and percentage of the total numbers and occurrence.

1 May 1981. Samples collected from the shore (n = 13)

CLASS INSECTA	Numbers		Occurrence	
	Actual	%	Actual	%
Order Diptera				
Chironomidae larvae	5	0.30	3	23.08
Chironomidae pupae inc. *Chironomus plumosus* *Polypedilum nubeculosum*	38	2.28	13	100
Order Coleoptera				
Unidentified larva	1	0.06	1	7.69
Order Trichoptera				
Unidentified larva	11	0.66	2	15.38
Order Megaloptera				
Sialis lutaria larvae	3	0.18	1	7.69
Order Hymenoptera				
Hymenoptera adult*	1	0.06	1	7.69
CLASS CRUSTACEA				
Order Amphipoda				
Gammarus sp.	16	0.96	4	30.77
Order Isopoda				
Asellus meridianus	1	0.06	1	7.69

Order Cladocera				
Daphnia sp.	1600	96.10	2	15.38
CLASS ARACHNIDA				
Order Acarina				
Unidentified Hydrachnella	2	0.12	2	15.38
CLASS GASTROPODA				
Order Mesogastropoda				
Potamopyrgus jenkinsi	5	0.30	2	15.38
Valvata piscinalis	25	1.50	4	30.77

31 July 1981. Samples collected from Cage IV (n = 9)

CLASS INSECTA				
Order Diptera				
Chironomidae pupa	1	50	1	11.11
PHYLUM CHORDATA				
Order Teleostei				
Perca fluviatilis (fry)	1	50	1	11.11

31 July 1981. Samples collected from the shore (n = 3)

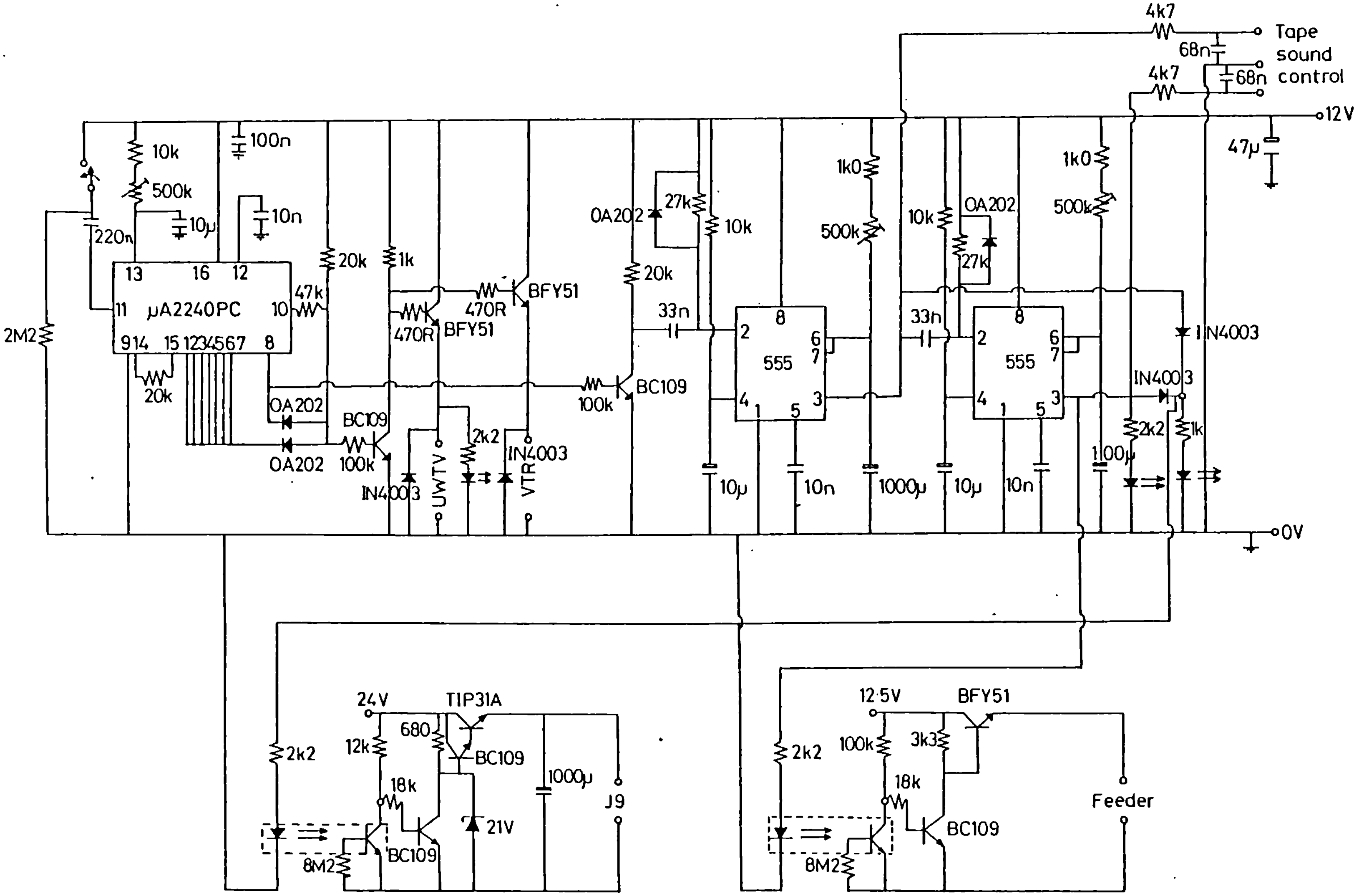
CLASS INSECTA				
Order Diptera				
Chironomidae larvae	46	29.68	2	66.67
Chironomidae pupae	9	5.81	3	100
Order Coleoptera				
Unidentified larvae	2	1.29	1	33.33
Dytiscidae adult	2	1.29	1	33.33
Unidentified Insecta larvae	1	0.64	1	33.33

CLASS CRUSTACEA				
Order Amphipoda				
Gammarus sp.	1	0.64	1	33.33
Order Isopoda				
Asellus meridianus	3	1.93	1	33.33
CLASS GASTROPODA				
Order Mesogastropoda				
Potamopyrgus jenkinsi	72	46.45	2	66.67
Valvata piscinalis	15	9.68	3	100
CLASS LAMELLIBRANCHIA				
Order Eulamellibranchia				
Pisidium sp.	4	2.58	1	33.33

APPENDIX C. A CIRCUIT DIAGRAM OF THE REMOTELY OPERATED TIMING MECHANISM.

The diagram shows the apparatus used in Loch Charn (Section 3) to remotely operate the underwater television camera (UWTV), video tape-recorder (VTR), loudspeaker (J9) and feeder in a programmable sequence. The sequence was initiated by a clockwork clock triggering the circuit at pre-set times.

The experiments in Dunstaffnage Bay (Section .2) used a similar apparatus except that the camera and video tape recorder were switched on manually from the laboratory.



4k7
Tape
sound
control
68n
68n
4k7
12V
47μ
0V
10k
500k
10μ
100n
10n
220n
2M2
μA2240PC
13
16
12
11
10
9
14
15
1234567
8
20k
47k
20k
1k
OA202
OA202
BC109
100k
IN4003
470R
470R
BFY51
BFY51
UWTV
2k2
IN4003
VTR
OA202
27k
10k
20k
100k
BC109
33n
555
2
8
6
7
4
1
5
3
10μ
10n
1k0
500k
1000μ
10k
OA202
27k
33n
555
10μ
10n
1k0
500k
100μ
IN4003
IN4003
2k2
1k
2k2
24V
12k
680
TIP31A
BC109
18k
BC109
21V
1000μ
J9
8M2
BC109
2k2
12·5V
100k
3k3
BFY51
18k
BC109
Feeder
8M2

APPENDIX D. A COPY OF THE ANGLERS' RETURN FORM USED DURING THE LOCH CHARN EXPERIMENTS (SECTION 3).

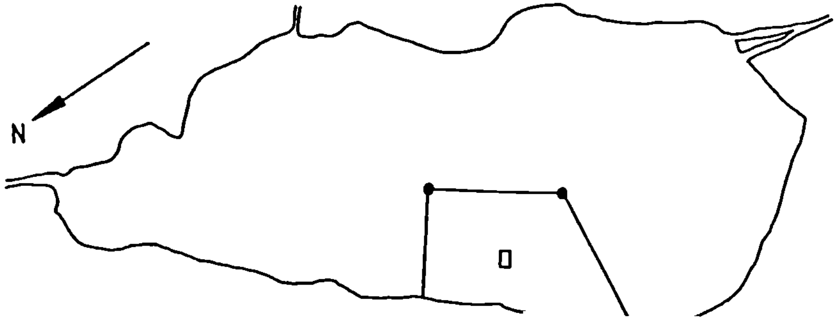
LOCH CHARN EXPERIMENT

1. DATE AND TIME OF VISIT ....

2. DETAILS OF CATCH. Please enter details in the table below.

TYPE (rainbow or brown trout)	TAG (enter number of fish tag)	METHOD OF CAPTURE (dry, wet fly, worm etc.)	WEIGHT (use scales provided)	SIZE LENGTH (ruler in box) (measure from snout to fork of tail to the nearest mm)

3. WHERE WERE THE FISH CAUGHT? Please mark the position of your catches on the map, using a B for each brown trout and an R for each rainbow trout.



4. WHAT HAD THE FISH BEEN EATING? Please fill in the boxes below with any observations you make of the diet of the fish you capture. The presence of artificial food will be indicated by a granular light brown paste in the stomach or exuding from the vent.

Type of Food	Natural	Artificial	None
Brown Trout			
Rainbow Trout			

5. REMARKS? Any remarks that you consider would be of interest will be appreciated.

Thank you for your cooperation.

APPENDIX E. RECOMMENDED FEEDING RATES FOR RAINBOW TROUT (% OF TOTAL FISH WEIGHT PER DAY).

Source : Edward Baker Ltd., Daily Feeding Guide.

Water temperature (°C)	Fish weight (g) 40-60	60-90	90-135	135-200	>200
5	1.2	1.0	0.9	0.8	0.7
7	1.4	1.2	1.1	1.0	0.9
9	1.6	1.4	1.3	1.2	1.1
11	1.9	1.6	1.5	1.4	1.3
13	2.2	1.9	1.7	1.6	1.5
15	2.5	2.2	2.0	1.9	1.8
17	2.6	2.3	2.1	2.0	1.9
19	1.5	1.2	1.1	1.0	0.9
21	1.1	0.9	0.8	0.7	0.6