Shoaling behaviour in the minnow and its effect on population structure and movements

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SHOALING BEHAVIOUR IN THE MINNOW
AND ITS EFFECT ON
POPULATION STRUCTURE
AND
MOVEMENTS.

by

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M.Sc. ECOLOGY DISSERTATION
UNIVERSITY OF DURHAM 1972
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SHOALING BEHAVIOUR IN THE MINNOW AND ITS EFFECT ON POPULATION STRUCTURE

AND MOVEMENTS

Introduction

Since Parr (1927) described shoaling behaviour in chub mackerel and killifishes in aquaria, and came to the conclusion that the behaviour he observed was a visual response to other individuals of the same species, there has developed an increasing interest in the manner in which, and the reasons why, certain fishes group themselves into masses generally referred to as schools or shoals. Nikolsky (1963) has produced different definitions for the two words. The shoal he defined as a more or less prolonged grouping of mutually orientated fishes, of closely similar biological conditions and age, united by similar behaviour. The school he considered to be a smaller grouping within the limits of a shoal, with the fish within the range of interaction of their sensory organs. In this study the two words will be used synonymously. Allee (1931) defined two main types of groupings in his investigations of the bases of social behaviour. The first type is the animal grouping that forms as a result of each member being attracted to the same region, owing to physical environmental conditions to which each individual shows a common response. His second grouping is based on the mutual attraction between species mates. This is exhibited in different degrees of intensity, animals being strongly, moderately or weakly attracted.

Allee's studies stimulated the subject of physiological advantages of community life, but up until 1946 only two studies were made on the phenomenon of shoaling (Spooner 1931; Shlaifer 1942). Breder and Halpern (1946) presented new thoughts and experiments on fish aggregations. Shoaling was considered an extreme form of the aggregating tendency. Distinguishing features of the shoal were - all individuals (a) similarly orientated, (b) uniformly spaced, (c) moving at uniform speed. In many species studies these precise definitions could not be rigidly applied, owing to the continuous state of flux, within the shoal, with respect to orientation, spacing and speed of movement. Morrow (1948) considered aggregation as "a chance grouping of individuals brought
into a given locality by external factors not concerned with relationships between individuals". Shoals were considered to be closely knit cohesive groups in which there appeared to be a definite centripetal influence existing between fish. Keenleyside (1955) defined the school as an aggregation formed when one fish reacts to others by remaining near them. Typical features shown were performance of the same activity at the same time, lack of aggressiveness between members and equality of rank.

The ideas which suggested this study provide three possible explanations for the shoaling phenomenon. These are:— (a) during the breeding season shoaling plays an important part in the reproductive activities of the species. Breder (1959) suggested that the shoal represents an operation by the population in order to ensure the possibility of reproductive encounters. (b) shoaling is an important factor in the location of locally abundant food items. Gee (1971) considered that shoal movements elicit prey flight activity thus facilitating detection of food. (c) shoaling affords a certain degree of protection against predation. Brock and Riffenburgh (1960) discussed the mathematical aspect of this approach, also shown by Olson (1964). A verbal interpretation has been provided by Breder and Halpern (1946), Hiatt and Brook (1948), Sette (1950), Springer (1957).

Shaw E. (1969) considered the attempt to find one single adaptive feature for shoaling was of little use, for shoaling in fish is probably due to the compounding of a number of adaptive features, three of which I suggest above. The possibility that shoaling is not an adaptive mechanism and that it could be expected to arise in any species subject to aggregation, has also been discussed. (Williams G. C. (1964)).

Shoaling behaviour in the minnow is one factor affecting the population dynamics of the species, producing changes in growth, fecundity, mortality and movements. Mann (1971) reported difficulty in obtaining accurate estimates of survival in the minnow, because in some months a shoal could be inside the study area, and in other months outside the study area. Gee (1971) also recognised the difficulty of sampling a fish population which has an unstudied
shoaling pattern. The size composition of catches of yellow fin tuna (Neothunnus macropterus) has been used in an attempt to determine growth, age and schooling habits - Schaefer (1948), and a similar method is followed in this study. Fish populations have powerful compensatory mechanisms. They are able to modify the density of the population, growth rate within the populations, as well as the fecundity. The effect of population density on production has been appreciated, but not well studied. A negative correlation has usually been found between density and growth rate. In stream and littoral species, both territorial behaviour and dispersion act together, with factors in the physical environment, to regulate the density of the species. In shoaling and pelagic species, the demonstration of the action of density dependent factors is difficult to demonstrate, though growth may often be inversely related to density. (Backiel & Le Cren 1966).

Fish populations are known to show remarkable powers of migration and dispersal, but studies have concentrated on salmonoids. The importance of movements on the dynamics of the species has been shown in other animal populations. Andrewartha and Birch (1954) discuss insect populations, whilst the whole subject of the effects of movements on the regulation of species numbers has been a topic of much controversy (Lack 1954; Wynne-Edwards 1962).

Workers with freshwater fish populations have reported an absence of extensive movements, a fact which will play an important role in the determination of abundance and production. In the Thames, roach (Rutilus rutilus L) perch (Perca fluviatilis L) and dace (Leuciscus leuciscus L) show a limited range of movement (Williams 1965). Marking experiments carried out by Le Cren in Windermere showed a tendency for marked Perch to return to their original site of capture (Worthington 1950), and added to the idea that the fish occupied a 'home range' (Gerking 1953). Hartley (1947) demonstrated a movement of roach into shallow water in order to spawn, whilst Stott B. (1967) produced evidence for a mobile and static component of roach (Rutilus rutilus L) and gudgeon (Gobio gobio L) populations. Movement may be vertical as well as horizontal and may take place on a daily basis as well as seasonal.
In this investigation it was decided to obtain visual information on the shoaling behaviour of the minnow, which, together with seine netting results, might provide an indication of its effects on the population structure and movements during the period of study. Visual observations of shoaling were investigated both in the field and in the laboratory. Routine weekly seine netting was carried out at two sites, to provide information on population structure over this period, whilst an attempt was made at estimation of population numbers of the minnow (*Phoxinus phoxinus* L), together with an estimate of numbers of a non-shoaling species, the stone loach (*Noemacheilus barbatulus* L). Movements of minnow shoals were recorded over a twenty four hour period.
Fig. 1. RELATIVE POSITIONS OF STUDY SITES.
1. Description of the river and sites

The River Wear forms at Wearhead from two small burns, Kilhope Burn and Burnhope Burn. At this point the river is 336 metres above sea level and 106.9 kilometres from Wearmouth Bridge, Sunderland. The river exhibits marked changes of flow throughout the year, in spite of compensation water released from upland reservoirs. Major floods have occurred at all seasons of the year and quite marked fluctuations in level were observed during the period of study, which extended from May through to August. A gradual increase in nutrient levels is observed (Whitton and Buckmaster 1970). Sewage effluents into the river have no marked effects on the general water chemistry.

Two sites were investigated on the River Wear:

(1) Croxdale (NGR NZ262374)  
(2) Finchdale Priory (NGR NZ294473)  
and one site on the River Browney:

(3) Langley Park (NGR NZ213453)

Site (1) Croxdale is wide and shallow, having a mean width of 30 metres and a depth of not more than 1.5 metres. Cladophora glomerata (L) covers much of the gravel areas during the summer period. In the shallow, slack reaches of the river much silt is deposited during the summer, and during floods large quantities of this are washed down. Just upstream of the sampling site is an extensive gravel bed, which remains uncovered during summer, except after periods of heavy rain. Site (2) Finchdale Priory has a similar width of 25-30 metres, but the river here runs through a deep gorge formed by the river, so that in mid-stream bare rock is exposed, and deep pools of 2-4 metres are present. Macrophytic growth is reduced, probably due to shading by trees in the gorge. The site chosen was an area of slack water with a gently shelving sandy bed. Site (3) Langley Park, used for many of the behavioural observations, is a slow flowing stretch of the River Browney, upstream of the weir and sewage effluent. The mean width of the river is 8 metres, and depth 1-1.5 metres, with the river bed formed from mud and silt material.
Fish species recorded at sites 1 and 2 are:

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phoxinus phoxinus (L) (minnow)</td>
<td>C</td>
</tr>
<tr>
<td>Anguilla anguilla (L) (eel)</td>
<td>C</td>
</tr>
<tr>
<td>Salmo trutta (L) (sea trout)</td>
<td>C</td>
</tr>
<tr>
<td>Gasterosteus aculeatus (L) (three-spined stickleback)</td>
<td>C</td>
</tr>
<tr>
<td>Noemacheilus barbatulus (L) (stone loach)</td>
<td>C</td>
</tr>
<tr>
<td>Gobio gobio (L) (gudgeon)</td>
<td>F.P.</td>
</tr>
<tr>
<td>Leuciscus leuciscus (L) (dace)</td>
<td>F.P.</td>
</tr>
<tr>
<td>Salmo gairdneri(R) (rainbow trout)</td>
<td>C</td>
</tr>
</tbody>
</table>

C = Croxdale                                    F.P. = Finchale Priory
2. General biology of the minnow (Phoxinus phoxinus) (L)

Ten species of Phoxinus are known in Eastern Europe and Northern Asia. The species Phoxinus phoxinus (L) is to be found in most of Europe, and belongs to the upper fast flowing reaches of rivers, ponds, shallow lakes, and the littoral areas of deeper lakes. It shows no real preference for substrate being found in waters with a sandy or stony bottom. It is often found in areas of slack water, where, during the period from April through to October, it will form shoals consisting of large numbers of fish. From November to March dispersal of the shoals occurs, the minnows remaining quiescent under stones in the slacker areas of the river. The minnow grows to a size of up to 10 cms, though sometimes specimens are recorded showing a greater length. The longest specimen recorded in this survey was 10.7 cms in length and weighed 19.4 gms. Mean lengths recorded for the different age groups are (Back 1940) O, 34.29 mm.; I 53.12 mm.; II, 69.39 mm.; III, 85.33 mm.; IV, 95.56 mm.; V, 113.83 mm. Females of age classes III and IV are larger than the males. Spawning occurs in the months of April, May, June and July when large spawning shoals are formed. At this time the male shows a characteristic spawning coloration, with the belly, the pectoral and pelvic fins turning reddish in colour, and the whole body assuming a darker coloration. Minnows show maturity in a few individuals at the end of the first year, and in the majority of individuals during their second year. Food consists mainly of freshwater invertebrates together with microscopic algae. They are preyed upon by larger fish e.g. trout, perch, pike and chub.
3. Behavioural observations of shoaling in the field

(i) Methods: Purely visual observations were carried out at three main sites,

(1) Croxdale

(2) Finchale Priory

(3) Langley Park, River Browney

together with several other sites on the River Wear. Only water temperature readings were taken and these only on a few occasions, as it was thought that factors such as light intensity and water flow are subject to the effects of many other variables. It is also believed that numerous factors are involved in the behavioural movements of fish - e.g. physiological state of the fish, time of the day, amount of cloud cover affecting both light intensity and water temperature. Photographic records were also made using a Prinzflex 500 camera, fitted with a Domiplan f 2.8 lens with polaroid filter.

It was found that the best conditions under which to observe and photograph shoaling behaviour, were prevalent on hot, cloudless days with a high light intensity. Observations were carried out during the period early May to early August, but there were few days throughout this period that were suited to both visual and photographic observation.

(ii) Observations

(a) Shallow water shoaling. During periods of fine weather as described above, shoals were frequently observed in shallow, slack areas of the river, close in to the bank. At Croxdale these shoals were observed in slack water both above and below the bend of the river. Large shoals were formed near the entry of Nicky Nack beck (Fig. 2) Shoals of the smaller size groups were present in the shallower water of 10-25 cms depth, whilst the larger size groups were positioned in water of 25-50 cms depth. Temperatures in these regions were 2-3°C above the temperatures in mainstream i.e. 15°C as compared with 11-12°C.
The entry of Nicky Nack Beck provides a situation of a colder body of water from the beck, moving into the shallow slack area of warmer water. On several occasions shoals were observed in this region, positioning themselves parallel to the incoming water from the beck.

During periods later in the summer i.e. late July and August, the fry maintained their shoals in shallow water areas and sheltered pools near to the banks, some of these pools not exceeding 2" in depth. Minnow fry were also to be found in the shallow slack pools in Nicky Nack Beck.

(b) Shoal movements. All shoals observed were in no way static in nature but were in a state of continuous flux. At the observation sites shoal movements took place both up and downstream. From these main shoals, members may move off (see plates 3(a), 3(b), 4(a), 5(a), 5(b)) as a result of which one of three activities might occur, (a) the breakaway group wheels round and rejoins the main shoal, (b) the group reshoals with members of a different shoal but of a similar size grouping, (c) the group forms a new shoal, which may or may not shoal with other shoaling groups at a later time. When dissociation from a shoal took place, all that was required to initiate this dissociation was a rapid movement of one or several fish away from the main shoal, eliciting a corresponding movement of more fish away from the main shoal. Fish midway between these two new shoaling units showed panic movements, in an attempt to reshoal and maintain contact with one of the two new shoals.

Movement of shoals along the length of the river appears to be restricted in nature, probably due to the fact that observable movements occurred mainly in areas of slack water which were themselves restricted. Observation of movements in deep water
areas was hindered by decreased light intensity, with increased depth and a reduced angle of vision from the observation point. At Finchale Priory minnow shoals showed more extensive visible movements than at Croxdale. At this site evidence for female spawning group movements was obtained by capture, using rod and line whilst being visually observed, of a group of minnows of size range 7.5 - 10.7 cm, consisting of II, III and IV year fish, of which seventeen were ripe females and two were mature males.

(c) **Nature of substrate and background coloration.** Shoals did not appear to show any preference for a particular substratum for different shoals were often found grouped over different substrates; both coarse sand areas and gravel areas appeared to be equally favoured. The colour tone of the background presented no real preference, for shoals maintained position over a wide variety of background tones. During periods of fine weather with a high light intensity, minnow shoals showed no tendency to move to cover areas, but remained either in shallow water areas or shoaled in the surface waters of deeper regions of the river. This behaviour was observed during the months of May, June and July, the spawning period of the fish and a time of high activity.

(d) **Feeding behaviour of shoals.** This was best observed during afternoon and evening periods. The minnow feeds mainly by day, and gut analyses of minnows sampled at different periods of the day showed a high proportion of guts empty during morning hours, with an increase in feeding activity during the afternoon and evening. Feeding activity was rarely observed before 1200 hours. For this reason the gut analysis sample, to be described under 3(ii), was
taken during the evening. As a result of feeding activity, the external uniform appearance of the shoal was broken down. Not all shoal members would be actively feeding at a particular point in time, and these would retain the uniform shoal appearance, each fish being a similar distance away from its neighbours and orientated in the same direction. Those feeding would be involved in active movements near to the shoal, some rising above the surface to obtain their prey (see Plate 8(a)) whilst others maintained a grazing action on stones, bottom muds or vegetation. Disruption of the uniform shoal appearance was brought about by a temporary localised aggregation of fish, as a result of rapid movement towards a food source by a single member or several members of the shoal. This movement took the form of a quick darting action followed by rapid lateral movements of the body on capture or attempted capture of the prey organism. This action could be repeated several times, for often the fish would reject the prey organism once or several times, and then make a further attempt at reingestion. Frequently these feeding movements elicited feeding movements of nearby minnows.

(e) Food intake by the minnow shoal. A gut analysis study was made on fish netted from Finchale Priory (15.6.72, 1930-2030 hours). Fish were placed in 4% formalin soon after death by suffocation. They were not placed into formalin immediately owing to the possibility of regurgitation on immersion. The following day the stomachs were removed and placed in 4% formalin in preparation for identification of food items. Each stomach was studied as a single unit. Several methods of analysis for stomach contents of fish are available. In this particular study both the "Frequency of occurrence" method and the "Points" method were used in order to provide a comparison of the results by the two methods. In the former of these the stomach contents were examined and each individual
food item identified and expressed as a % of the total number of stomachs examined. Unlike electro-fishing, this method of sampling by seine netting was not size selective during the sampling period, and there was no evidence that it selected fish which had been consuming a particular type or quantity of food. Capture by hand net showed similar gut analysis results. The stomach of the minnow is not easy to distinguish from the rest of the alimentary canal and so only the anterior one third of the alimentary canal was examined.

The 'points' method (Swynnerton and Worthington 1940, Frost 1943, Hynes 1950) was found to be the most useful. Percentage occurrence values often give misleading results, high values being recorded for the presence of single food items. For the 'points' method stomach contents were removed, identified and each food type was allotted points, depending upon its size and abundance. The total points allocated per fish were dependent upon the size of the fish and divided up as follows:

<table>
<thead>
<tr>
<th>Minnow size (cms)</th>
<th>2.1 - 4.0 cms.</th>
<th>4.1 - 6.0 cms.</th>
<th>6.0 cms+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gut fullness</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>⅛ full</td>
<td>15</td>
<td>20</td>
<td>25</td>
</tr>
<tr>
<td>⅜ full</td>
<td>30</td>
<td>40</td>
<td>50</td>
</tr>
<tr>
<td>¼ full</td>
<td>45</td>
<td>60</td>
<td>75</td>
</tr>
<tr>
<td>Full</td>
<td>60</td>
<td>80</td>
<td>100</td>
</tr>
</tbody>
</table>

All points gained by each food item were summed and presented in % form to give the percentage composition of the food of all the fish examined. This points method is essentially an approximate volumetric method. Its limitation is the subjective allotment of points by the investigator.
Results: Chironomids formed the most important part of the diet for minnows of all the arbitrary size groupings see Fig. 4 and Table 1. Insufficient fish, of sizes 2.1-4.0 cms and 6.1 cms upwards, were captured to provide a reliable comparison of the food intake by the different sizes of fish. Results indicate that the minnow shoal was occupying a region where chironomids were particularly abundant. Mann and Orr (1969) found little variation in the food composition of different size groups of minnow, stickleback and salmon. There is an indication with this study, that minnows of above 6.1 cms in length were taking a higher proportion of terrestrial organisms, e.g. diptera. Chironomids formed a smaller part of the diet in this group as compared with the other two groups.

(f) The 'fright reaction'. The alarm or fright reaction, in response to movement on the bank or object disturbance in the water, produces initially a denser aggregation than is present in the normal shoaling behaviour exhibited prior to the disturbance. During this period of rapid movement shoal members often break surface. This is thought not to be a necessary composite of the fright reaction, but is probably a consequence of the over-aggregation. The following response is a movement of the shoal in its more compact form along what appears to be defined routes, i.e. the fish moving as a shoal, possibly splitting into two or three separate parts, but never showing a complete dispersion. If this movement carries them into the mainstream then dispersal of the shoal takes place as a result of the rapid water movement in this area, producing an inability of the individuals to maintain shoaling behaviour. Return to the original shoaling area occurs not long after dispersal and is
dependant on the intensity and length of disturbance. The sub
groups show no evidence of the over-aggregaton of the dispersing
panic group. The returning members of the shoal arrive in small
groups and exhibit a preliminary backward and forward movement
over the shoaling area before reformation is accomplished.

Shoals of different sized fish show different reactions to
changes in the environment. When the 'fright reaction' of the
larger fish is induced by movements of the observer, the smaller
fish remain undisturbed requiring a much greater disturbance, such
as water body disturbance, to promote the fright reaction. The
fishes of these different shoals, therefore react in different
ways to changes induced in their environment, whilst individuals
of each shoal react in the same way.

(g) **Pod formation.** This behaviour may have associations with the
'fright reaction' in that it could be protective in nature, but
was only observed during periods of fine weather and high light
intensity. The fish shoal takes on a ball shape with insufficient
clearance for swimming, leading to contact between individual fish.
Once formed no large movements take place within the pod or by the
pod, the fish remaining nearly or completely randomly orientated,
often situated in the same spot for a period of up to five minutes.
Pod formation is often initiated soon after local disturbance, but
is also observed when shoals make close contact with objects present
in the water, such as tree branches or decaying vegetation. (See
plates 6(b), 7(b), 8(b)).

(h) **Mill formation** was observed under similar conditions to pod formation.
The activity took place in the surface waters of the river with the
fish exhibiting circular swimming movements for periods of up to two minutes and then moving off. It is thought that by these circular swimming movements the members of the shoal are able to conserve energy though no satisfactory reason for the mill formation has been put forward. The formation of the mill may be intrinsic in that the shape that a shoal takes may elicit the milling behaviour, or extrinsic in that it is produced by one or several transient factors, such as light intensity, temperature or chemical. (See plates 4(b), 6(a), 7(a)).

(i) Shoal formation with other fish. On one occasion several stone loach (Noemacheilus barbatulus L) were observed shoaling in with a minnow shoal of similar sized fish. The stone loach is a poor swimmer and was unable to maintain a constant position within the shoal, which was remaining quite stationary. The loach, which are bottom dwellers, were positioned near to the base of the minnow shoal in shallow water.

During the period late July to early August fry were present at the Croxdale and Langley Park sites. Large numbers of fry were shoaling close in to the bank, with both minnow and stickleback fry present within these shoals. There appeared to be no separation of individuals of the two species within the shoals. From middle to late August the stickleback no longer played a part in the formation of these shoals, but showed a more dispersed distribution.

Possible evidence for shoaling with other species, was also provided from netting results. At Croxdale site on three occasions fingerling trout (Salmo trutta L) were netted with the minnows. Muus B. and Dahlstrom P. (1971) state minnows are often found in shoals with trout or salmon parr of an equal size.
(j) Shoal composition. As an aid to the identification of shape and composition of the shoals, photographic data collection was undertaken. This provided information on the numbers of individuals within the shoals, the relative sizes of the fish within the shoals, together with an indication of the wide variety of shapes exhibited by the shoal (see Plates 5(a,b)). A high proportion of the shoals photographed were formed from individuals at the beginning of their second and third year of life (I and II), only II year fish being fully mature. It was only this section of the population that were seen to exhibit mill and pod formation, although 0 year fish were present in the same area and at the same time. Shoal numbers showed a maximum of 400 - 500 fish, though shoals with numbers well below the maximum were also observed (See Plates 3(a), 3(b)).

(iii) Conclusions and discussion: Several theories have been put forward to explain shoaling behaviour in fish. From the observations described above one can obtain an indication of the lines of thought which have led to these various theories. They can be considered under three main headings:

(a) Shoaling affords a certain degree of protection against predation. It may be that shoal formation is not an adaptive mechanism but is a consequence of adaptive behaviour on the part of the individual, i.e. shoaling is a form of shelter seeking. The extreme form of this behaviour may be exemplified by the pod formation observed in this study. Reduction in the area in which members of the species are present may act as a factor in reducing predation. This might explain the frequent pod formation observed near to tree branches present in the water, as a form of camouflaged concealment.

Springer (1957) reports similar pod formation in Jenkinsia and Lagodon, both marine species, and suggested a description for the shoal as being a large creature which presented an example of collective mimicry, and which Springer thought
provided protection by its frightening appearance.

Shoaling species of fish are not climax predators at the end of a food chain, but are prey species for a large part of their life history. According to various anglers questioned, the minnow formed a common item in the diet of sea and rainbow trout in the River Wear. These predators at the end of a food chain are ordinarily non-shoaling solitary fish. If shoaling does afford some protection, this may be a result of scattered prey being more liable to detection. Large shoals may have a deterrent influence over approaching predators. One would not expect this to be a long lasting influence owing to habituation by predators, which could lead to an increase in the numbers of predators in the area. This would become an important factor in the disintegration of the large group. Maximum shoal sizes observed at Langley Park and Finchale Priory, being in the region of 400-500 fish, were similar to those seen at Croxdale, though more shoals were present at the latter area. Large shoaling groups may give rise to a 'confusion effect' (Allee 1938) whereby predator fish show a reduced food intake if too many food objects are presented. More experimental work is required to produce evidence for the survival value of the 'confusion effect'.

Protection advantage may also be provided by chemical substances in order to communicate alarm to other members of the shoal. The 'Schreckstoff effect' (Pfeiffer 1962) (also see p. 22) has only been reported for damaged and injured fish as observed with the minnow in this study. It is believed that the alarm reaction is a purely visual reaction and not chemically induced. The 'Schreckstoff reaction' is largely confined to members of the Cypriniformes and members of this group are not considered as obligate shoalers.
It may be that movements into shallow water provide some protection against predators, and evidence to be presented in section 7 suggests that this is probably the case.

(b) Shoaling is an important factor in the location of locally abundant food items.

Minnows at the site studied, and at the time of study, were mainly feeding on one food source i.e. Chironomidae in the form of larvae, pupae and adults, preference being for the larvae which were present in 62 out of 114 stomachs examined. From observations over a period of several weeks at the Finchale site it was noted that minnow shoals moved into this particular area at approximately 2100 hours, an observation which initiated the 24 hour study. Many fish could be observed actively feeding on the river bed (see notes on feeding behaviour in the shoal). The shoaling behaviour may have the effect of reducing the variety of diet. Maitland (1965) found that the major items in the diet of minnows, in the River Endrick, were algae, but also adds that in this situation the minnows browse non-selectively on Aufwuchs communities (Ruttner 1953). Frost (1943) identified Cladocerans as the main food source in Windermere, with Copepoda, filamentous algae and diatoms also forming a high proportion of the diet. At her other study site, the River Brathay, minnows were chiefly feeding on filamentous algae with Chironomid larvae next in importance. Badcock (1949) found that desmids, diatoms and filamentous algae were predominant in the minnow stomachs that were examined; whilst Hartley (1948) reports a preponderance of Insecta with 26.5% (by occurrence) of the diet being formed by Chironomids. Mann and Orr (1969) also provide details showing a restricted range of diet during the spring and summer months, when shoaling occurs. Gee (1971)
found Chironomidae and Ephemeroptera to be the major constituents. Evidence suggested, however, that feeding was largely non-selective and that fish tended to seize any small moving object. He added that during activity in the shoal, minnows disturb prey into flight movement and that the roaming nature of the shoal adds to the possibility of coming across larvae or emerging adults. Manteifel and Radakov (1960) have shown experimentally, that when one part of a shoal saw food and made towards it, the remainder of the fish in the shoal were attracted by this movement even though they were unable to see the food. Similar observations were made by myself in the field. It seems therefore that shoaling may facilitate the location of food items.

Little is known at the present moment of the effects of shoaling species of fish on production within their environment, as well as the contribution to production by these species. A significant feature of the few production estimates that have been made is the large contribution made by small or young fish.

The tendency for an increase in the size of a shoal may be limited by depletion of food. A restricted shoal size is suggested by the photographic evidence, though at Croxdale even though these approximate sizes were maintained, several shoals were present in short stretches of river.

(c) During the breeding season shoaling plays an important part in reproduction. Shoaling may be considered a means by which members of the same species remain together, and ensures the possibilities of contact between mates during the spawning period. A restricted spawning season requires that mature species members come together within spatial and temporal limits in order that mating may take place. During this study large numbers of one and two year old fish were observed and netted shoaling in large numbers during the spawning period. Many
members of these shoals exhibited nuptial colouring and occupied shallow areas of water. Woodhead P. M. J. (1956), when examining minnow behaviour in a light gradient, demonstrated extremely active behaviour at high light intensities and no sign of a light intensity limit during the spawning period. This probably explains the shallow water shoaling observed at this time. Large shoals of minnows formed near the entry of Nicky Nack beck, which may act as an additional spawning ground, besides regions in the river itself. The extent to which both these areas are used for spawning is unsure. Both fry and one year old fish were observed in the beck, though no mature two year old fish. This behaviour prior to spawning is not uncommon in fishes. In the marine fish, the grey gurnard (Trigla gurnardus), spawning takes place from April to August and it is thought that the surface swarming displays have important connections with reproduction. The pod and mill formation in the minnow should be examined further, and their possible importance in connection with reproductive activities traced. The actual timing of spawning was not clear and in the minnow is known to extend over three months. Fully ripe females were netted in the months May, June and July. As stated above (P.10) evidence for female spawning groups was obtained by capture of a shoal of minnows of size range 7.5-10.7 cm, consisting of 17 mature females and two mature males (Table 3). This is in contrast to evidence produced by Frost (1943) and Mottram (1922) who observed large numbers of mature males in the company of one or two females.

It is concluded that no one adaptive value can be assigned to shoaling and the values involved vary at different ages and stages during the life cycle of the animal. The proposed adaptive values from this study are (a) protection (b) food capture (c) spawning. Further adaptive values of migration and energy conservation have also been suggested.
4. Behavioural Observations in aquaria

(i) Visual Observations

(a) Methods: Shoals of the species *Phoxinus phoxinus* (L) were studied in aquaria. Fish held in the laboratory were fed daily on a diet of freeze-dried tubifex worms and one other commercial dried fish food preparation. Descriptions and observations were made during the period May to August, 1972. Fish were retained in aquaria of size 59.0 x 28.0 x 29.5 cms, containing tap water to a depth of 23.0 cms and maintained at a temperature of 16°C for the experiments. The River Browney and River Wear, County Durham were used as a source of fish for the experiments. It was found useful to make some general observations, initially on the shoaling behaviour, before proceeding with controlled experiments. The fish were allowed a 7-10 day period of acclimatization before observations and experiments were carried out.

(b) Observations: Shoals observed in the laboratory do not show a constant form. All fish in the shoal do not swim at the same speed. The more active fish in the shoal maintain contact with the shoal by swimming a more irregular path. In a stationary shoal some of the fish remain quite still whilst others swim slowly around, continually turning back on reaching the periphery of the shoal. Only in the moving shoals does extreme uniformity become apparent. If this were not the case, then shoal structure maintenance would be difficult.

The main feature of the shoal is that each individual reacts to fellow species members by remaining in their proximity. Any fish which move off from the main group often stop, turn and make their way back to the main group. When several fish show a movement away from the main shoal it is either followed by a return movement to the main shoal or a movement by the rest of the main
shoal following the breakaway group to a new shoaling position. During movement of the shoal most of the fish are orientated in the same direction. The speed of movement varies within the shoal with stragglers showing faster swimming movements in order to maintain contact with the main group. Fish in the shoals show a tendency to spread out in the horizontal plane during movements. Rarely were moving shoals observed more than a few fish deep.

There is no apparent leader to the shoal and no indication that larger fish have a greater attracting value for the other fish. A continuous interchange of leading fish was noticed. It may well be that greater activity by a fish may elicit following by other fish, for members of the shoal often follow other fish which show sudden and rapid movements.

The 'fright reaction' was also observed in the laboratory, taking a similar form to that described under field conditions. With movements of the observer, the fish rapidly form a dense aggregation in one corner of the aquarium. With removal of the disturbance the shoal gradually takes on its original form. Another aspect of the fright reaction is shown on replacement of a skin damaged minnow into the aquarium. This is accompanied by rapid, panic movements with aggregation in a part of the aquarium away from the replacement region. This mechanism has been recognised as part of the 'Schreckstoff reaction', investigations of which have been reviewed by Pfeiffer (1962). It has been established for many of the Cyprini forms, that an injured individual produces a chemical substance that is responsible for the inducement of the fright reaction in other individuals. A panic reaction is also observed when depth of water in the aquarium falls below a certain level, this level being higher for the larger fish than the smaller fish.
Dispersal of the shoal took place during late evening and night hours, a fact which has frequently been reported (Woodhead 1956, Harden-Jones 1956, Breder 1959).

(ii) Experimental observations

(a) Methods: Experiments were carried out in aquaria (dimensions as described above) with water temperature maintained at 16°C under conditions of minimum disturbance.

Methods employed were similar to those used by Keenleyside (1955) and are concerned with the importance of vision in shoaling. A glass jar was placed inside the aquarium at one end. Five minnows were placed into this jar and one test fish placed into the main aquarium at the centre. Time spent by the fish in each section of the aquarium (A and B) was then recorded over a period of fifteen minutes. The jar was then moved to the other end of the aquarium and the experiment repeated. This was repeated for two more test fish of similar size, together with an identical procedure for smaller and larger test fish. Frequencies in time are represented in minutes.

(b) Results. In order to determine whether the fish showed any preference for remaining in one end of the tank a $\chi^2$ analysis was implemented in order to demonstrate any significant difference in the time spent at either end of the tank both when the shoal is present at the end and when absent from the end.

'Null Hypothesis that there is an equal preference for each end of the tank'.
Total length of time of fish in A: 139.12 mins.

Total length of time of fish in B: 130.88 mins.

Number of tests: 9

\[ \chi^2 = 0.2516 \text{ Not significant} \]

Small sized test fish - lengths 2.8, 2.5, 2.7 cms.

Shoal fish - lengths 4.5, 4.7, 4.5, 4.6, 4.4 cms.

Species of test fish - Phoxinus phoxinus (L)

Species of shoal fish - Phoxinus phoxinus (L)

Total length of time in shoal area: 77.60

Total length of time in non-shoal area: 12.40

Number of tests: 6

\[ \chi^2 = 47.234 \text{ significant at the } .1\% \text{ level} \]

Equivalent sized test fish - lengths 4.5, 4.6, 4.5 cms.

Shoal fish - lengths 4.5, 4.7, 4.5, 4.6, 4.4 cms.

Species of test fish - Phoxinus phoxinus (L)

Species of shoal fish - Phoxinus phoxinus (L)
Total length of time in shoal area 77.96
Total length of time in non-shoal area 12.04
Number of tests 6
\[ \chi^2 \] 48.283 significant at the .1% level

Larger sized test fish - lengths 4.5, 4.7, 4.5 cms.
shoal fish - lengths 2.8, 2.4, 2.6, 2.5, 2.7 cms.
species of test fish - Phoxinus phoxinus (L)
species of shoal fish - Phoxinus phoxinus (L)

Total length of time in shoal area 64.52
Total length of time in non-shoal area 25.48
Number of tests 6
\[ \chi^2 \] 16.640 significant at the .1% level

The data for the equivalent and smaller sized test fish was then grouped in order to demonstrate any significant difference between the tendency to shoal as shown by the larger test fish and the tendency to shoal as shown by the grouped data.

'Null Hypothesis 'that the larger sized test fish show an equal tendency to shoal as compared with the equivalent sized and smaller sized test fish.
\( \chi^2 \) analysis indicates a greater tendency to shoal is shown by the equivalent and smaller sized test fish.

Similar experiments were attempted, placing five stone loach (Noemacheilus barbatulus L.) in the inner jar in order to determine whether a minnow does, or does not, visually distinguish between some other species and its own.

- Large test fish - lengths 4.5, 4.6 cms.
- 'Jar' fish - lengths 3.8, 3.6, 3.7, 3.8, 3.2 cms.
- Species of test fish - Phoxinus phoxinus (L)
- Species of 'jar' fish - Noemacheilus barbatulus (L)

Null Hypothesis - 'that the test fish shows an equal tendency to remain in each part of the tank'.

<table>
<thead>
<tr>
<th></th>
<th>Grouped data</th>
<th>Larger sized test fish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length of time</td>
<td>155.56</td>
<td>64.52</td>
</tr>
<tr>
<td>in shoal area</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length of time</td>
<td>24.44</td>
<td>25.48</td>
</tr>
<tr>
<td>in non-shoal area</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\( \chi^2 = 8.653 \) significant at the 1% level.

Total length of time in shoal area: 40.84

Total length of time in non-shoal area: 19.16

\( \chi^2 = 7.832 \) significant at the 1% level.
small test fish - lengths 2.7, 2.8 cms.
'jar' fish - lengths 3.8, 3.6, 3.7, 3.8, 3.2 cms.

species of test fish - *Phoxinus phoxinus* (L)
species of 'jar' fish - *Noemacheilus barbatulus* (L)

Total length of time in shoal area 45.52

Total length of time in non-shoal area 14.48

$\chi^2$ 16.06 significant at the 0.1% level

Both large and small minnows show a significant tendency to shoal with stone loach, with small minnows showing a greater tendency to do so than do large minnows.

Experiments were also carried out in order to determine whether the minnow shows any preference for a large shoal or a small shoal of fish of the same species. For this study one glass jar was placed at each end of the aquarium and different numbers of minnows placed in each jar as follows:

<table>
<thead>
<tr>
<th>Number of fish in area A</th>
<th>Number of fish in area B</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>

One minnow was then placed in the aquarium and the time spent in each half of the aquarium noted.
Null Hypothesis - 'that the minnows show an equal tendency to remain in each part of the tank'.

(1) Total time in A 29.997 $\chi^2 = 2.443$ Not significant
Total time in B 15.003 $\chi^2 = 2.443$ Not significant

(2) Total time in A 26.16 $\chi^2 = 0.8891$ Not significant
Total time in B 18.84 $\chi^2 = 0.8891$ Not significant

(3) Total time in A 23.43 $\chi^2 = 0.0385$ Not significant
Total time in B 21.57 $\chi^2 = 0.0385$ Not significant

(c) Conclusions
Results show that the test fish remains for most part of the time in that part of the aquarium in which the other fish are present. For much of this time it remains swimming near to the inner glass jar. The main points to be noted from the results are:

(1) The test fish show a definite attraction to the group of shoaling fish.
(2) Small test fish show a greater tendency to shoal than do large ones.
(3) Test fish attempt to shoal with another species of fish, with the greater tendency being shown by the smaller test fish.
(4) Test fish attempt to shoal with the larger of two shoaling groups, though a significant relationship is not shown.

These experiments verify the importance of vision in shoaling. Larger fish show a reduced tendency to shoal and this may be because
the larger a fish is the less likelihood of it falling prey to a predator species. If shoaling does have a protective basis then this latter idea would follow from this. Berwein (1941) observed that shoals of Phoxinus drove away shoals of individuals of smaller sized fish. This was not observed during these studies, either in the laboratory or in the field nor was there any evidence for a hierarchy between shoals or between members in the shoal. Berwein also noted that smaller sized minnows tend to keep near the surface, a point which was also observed during these experiments and which is probably based on the pineal influence in shoaling, larger and older fish having more fully covered pineal areas.

A factor that must bear importance in relation to shoal formation is the length of the fish. This factor could not be demonstrated under laboratory conditions but Bainbridge R. (1958) has shown that the speed at any particular frequency of tail beat is directly related to the length of the fish. The distance travelled per tail beat is directly dependant upon the amplitude of the tail beat. Thus it would seem that the smaller fish would be unable to maintain contact with larger members of the shoal during periods of rapid movement. Cushing and Harden-Jones (1968) state that fish cruise at three lengths a second. A short period of activity during the morning would therefore separate the fish out into shoals of various sizes.

Visual stimuli and lateral line stimuli must also indicate to the fish, changes in the velocity of other members of the shoal, and enable the fish to take up a particular position within the shoal. Many shoaling fishes, including the minnow, possess laterally farsighted eyes which may be adequately suited to the dark light contrasts which they are presented with. The lateral dark line along the length of the minnow is another possible aid to shoal maintenance. Denton and Nicol (1966) discuss the importance of the reflective layer in silvery
teleosts in camouflaging fish. Many shoaling fish, including the minnow, exhibit reflectivity this producing a conflict between the requirement to remain invisible to predators, and the need to see each other in order to shoal.

Dispersal of the shoal, observed at night in the laboratory, also indicates the necessity of the visual response. Woodhead (1956) and Harden-Jones (1956) produce descriptions for the behaviour of minnows under light gradients, which are of importance in connection with observations to be discussed under section 7. The latter observer recorded dispersal of a minnow shoal between light intensities of 0.024 and 0.0034 m.c.

Of other systems which may have possible importance is the olfactory sense, this is probably due to the interest shown in the schreckstoff reaction. Chemical stimuli, unless they are associated with water movements are, however, non-directional, and as compared with visual responses would produce a slow reaction time.
Population studies of the minnow

(i) Methods: Seine netting was carried out at weekly intervals at two sites on the River Wear. (1) Croxdale.  
(2) Finchale Priory.

The seine net was constructed from Rokolene windbreak netting 6.5 metres in length and mesh size 17 x 28 per 10 cm. Nettings were made between 1900-2100 hours. During this period it was found that large numbers of minnows shoaled in the study areas. Fish obtained from the netting at this time were suitable for stomach content analysis. Fishing was with the current in those areas with sluggish flow and against the current in areas with more rapid flow. More efficient netting was possible when the net was equipped at each end with a pole that was greater than the height of the net. As the site at Croxdale held a much larger population than that at Finchale, and the river bed possessed a sandier substrate and was relatively snag free, it was found that only one sweep was required to produce a good sample of the population in the area. Seven to eight hundred fish were often netted in a single sweep. These fish were placed into a 9.2 litre bucket filled with water, which was then stirred so that the fish were well distributed throughout the water. The fish were then quickly poured away until a sample of approximately two hundred fish remained. It is believed that this method of sampling produced a reliable sample of the catch.

Netting at Finchale Priory was more difficult, in that the river bed sloped away more rapidly and more snags were present thus reducing the netting efficiency and increasing the netting effort. Four sweeps were normally required to provide a reliable sample of the fish present in the area.

Fish thus obtained were allowed to suffocate and then placed into 4% formalin solution for 3-4 days to allow fixation of the material. After fixation the lengths, weights and sex of each fish was noted.
Fork length of the fish was taken measuring from the anteriormost extremity of the fish to the tip of the median rays of the tail. Weight in fishes has been taken by several different methods e.g. specimens that are alive, anaesthetized, freshly dead or preserved in various ways. Weights of fresh and preserved material are not comparable. Owing to the large numbers of fish handled and the information required from each fish it was found necessary to use preservative. Specimens preserved in formalin were treated consistently in this respect. For sex determination the gonads of the fish were inspected. In adult females the eggs were readily discernible in the ovaries whilst in the males the testes were smooth white in colour and non-granular in appearance. In some of the adult fish sexual dimorphism was observed both in colour and body proportions but it was found more reliable to internally examine the fish.

Age determination for the minnow is difficult, owing to the protracted spawning period. Gee (1971) attempted age-determination of River Wear minnows using several methods - e.g. scale structure, otolith examination, and the method of Petersen relating length frequency distributions to year classes. None of these methods did he find to be very satisfactory, so he concluded that the range of lengths in minnows of different year classes, as provided by Frost (1943), showed close approximation to the River Wear situation. This would appear to be the case, although slight variation will occur from year to year and with locality.

Sampling at both sites was carried out over a period of eight weeks from the 17 May to the 14 July, 1972. From a study of the length frequency histograms it is believed that overfishing was not taking place.

Year groups to be quoted below are designated symbols as follows:
(ii) Results: Details of length frequencies for the two sites are presented in histogram form (1) Croxdale site (Figs. 5 to 9)
(2) Finchale Priory site (Figs. 10 to 15)

Netting captures at the two sites produced fish mainly from two year classes, I+ and II+, although individuals of year classes III+ and IV+ were also netted. Fish of lengths 50-60mm showed a higher proportion of ripe eggs in the ovary as compared with fish of lengths 40-50mm. Fish examined having lengths less than 40mm showed a very low proportion of ripe eggs throughout the period of netting. Ripe minnows were present in samples taken for both sites up until late July. Data obtained from the capture of a shoal of spawning females is provided in Table 3.

Sex ratios of the samples (Table 2) show a significant departure from a 1:1 ratio on three occasions during the period.

Young first year fish appear first in the netting samples at Finchale Priory on the 28 June, but do not appear until after the period of routine sampling at Croxdale i.e. 22 July. Log length – log weight regression analyses for (a) fish lengths 0.55mm and (b) 56+mm are shown in Tables 4 and 5.

(iii) Conclusions: Examination of the length frequency histograms appears to suggest that the population size structure at the two sites studied, varied little over the sampling period. Shoals in the areas were formed to a large extent from I+ and II+ fish. A high proportion of those over a length of 50mm were found to be sexually mature. Fish tend to mature at a particular size rather than a particular age. In the minnow, due
to the wide variation in length within year classes, some one-year old fish are capable of breeding but do not exhibit their full reproductive potential until the end of the second year, the faster growing fish maturing earlier than the slow growing ones. A shoal of fully ripe females, together with two males, was captured on the 22 May, using rod and line whilst under visual observation at Finchale Priory. Evidence for spawning groups from other authors seems to contradict this observation. Frost (1943) records large numbers of males accompanying a few females in spawning livery. Hottram (1922) observed a preponderance of males on the spawning shallows with the females collecting in a pool below, only visiting the spawning beds a few at a time. The observation at Finchale may be explained as a movement of ripe females onto the spawning areas. This shoal present in the study area produced the earliest fully ripe females, smaller females obtained in the main sample, being not fully ripe.

The sex ratio in the adult part of a population is usually in the region of 1:1, although it is known to vary to some degree in fish populations. A significant variance from this ratio is observed for three occasions, during the weekly sampling. In each case a significantly higher number of males is present in the samples. It is unlikely that the methods employed are selective in capture, to the extent observed. One might expect a higher proportion of female fish to be caught at this time of year, owing to their larger size and reduced ability to evade the net. Notable, is the significant variance shown on consecutive days at the two sites. This could indicate a period during which conditions were suitable for spawning. Two reasons may be put forward to explain the phenomenon:

(a) during spawning a surplus of males is present on the spawning grounds.

(b) Movement of ripe females to spawning areas may occur. Evidence for
movements of ripe female groups is presented above.

Frost (1943) reports variance in the sex ratio in favour of female minnows, 63% as compared with males 37%. This was a constant factor throughout the year, and she concluded that it might be explained by the fact that female minnows tend to live longer than males. This latter observation has also been noted in this study, without any noticeable effect on the sex ratio. She also suggests that sex reversal as demonstrated by Bullough (1940) may be a contributory factor. This would again only produce a long term variation in the ratio.

Differences in time of arrival of young first year fish could be due to:

(a) differences in the time of spawning.

(b) differences in the distance of the study area from spawning sites in the river or inflow streams.

At Croxdale it is believed that a proportion of spawning occurs in Nicky Nack beck, an inflow stream downstream from the study area. Young first year fish were present in this beck during July and August and movements of young fish take place from the beck into the main river.

At Finchale Priory no inflow stream occurs near to the study area, and it is suggested that spawning occurs in suitable areas in the main river, possibly explaining the earlier arrival of first year fish.

Although little variation in size structure of catch was demonstrated until influx of young fish occurred, there is the possibility of interchange of individuals between adjacent stretches of the River Wear. Upstream movement would appear to be restricted by rough water areas and weirs. In this study it was observed that riffles appeared to restrict movement of shoals, fish maintaining positions in slack water areas. Movements downstream may occur by active swimming or by passive movements as a result of floods. Evidence produced by Gerking (1953), Stott (1969) and Williams (1965) indicate a restricted range of movement.
of roach, gudgeon and perch, but suggest the presence of a migratory component of the population. Mark and recapture studies (section 6) demonstrate the stability of the shoal over a short term period. Elaborate mark and recapture techniques would be required to follow movements during a long term study.

A reduction in the numbers of fish netted was noted after the spawning period. Scott (1964) reports that during the month following spawning, minnows were difficult to find and had apparently taken to deeper water. At this time they were in poor condition many being infected with Saprolegnia and bearing wounds resembling eel bites. Heavy mortality occurs over this period. Fish netted in this study after the spawning period, although fewer in number, showed no sign of being in poor condition.

The tendency shown by the minnow to shoal within certain size groups, has important implications in design of a sampling procedure for determination of the range of size classes in the population. The size composition of the total sample must be representative of the size composition of the population. It is necessary that each size class should be represented as a proportion of the total number of members of that size class. The shoal should be considered the basic unit of sampling, with samples from a large number of randomly chosen shoals providing a reliable estimate of the population structure. In this study as wide an area as possible was netted, in order to increase the likelihood of capture of a larger number of shoals. The presence of shoals of various size classes at the time and place of netting also aided this procedure. Section 7 indicates the importance of time in relation to the sampling programme. Gee (1971) considered his samples to be reliable estimates of the representatives of the shoal, but owing to the methods used i.e. minnow traps - probably failed to obtain a reliable sample of the population.
In fishes the length-weight relationship is represented by

\[ W = aL^b \text{ or } \log W = \log a + b(\log L) \]

For this study log weight was plotted against log length and the regression line calculated by the least squares method (Tables 4 and 5). The coefficient \( a \) is known to show considerable variation seasonally, with time of day and between habitats. The value of \( b \) is nearly always between 2 and 4, often being very close to 3. A value which is significantly different from 3 indicates allometric growth, i.e. as the fish grows larger it shows a proportionately greater increase in weight as compared with length. Values of \( b \) show a significant departure from 3, only for fish of 55mm and below at Croxdale whereas both length groups show significant departure from 3 at Finchale Priory though not for every sampling occasion. Differences in the length weight relationship may be due to maturity and sex of fish, season and changes in stomach fullness. Owing to the protracted spawning period it is unlikely that one would be able to obtain a date for the spawning time by reference to changes in the value of \( b \).
6. MARK AND RECAPTURE STUDIES OF MINNOW (*PHOXINUS PHOXINUS* L) AND STONE LOACH (*NOEMACHEILUS BARBATULA*) AT SITE (1) CROXDALE

(i) Methods: Croxdale site (1) was chosen for an investigation of minnow and stone loach populations because the area was relatively snag free, the gravel substrate proving no real hindrance to the netting efficiency.

(a) Minnow - mark and recapture. One sweep was made with the seine net covering an area of 50 square metres. On netting, fish were immediately marked by clipping the left pelvic fins. It is essential that the marking technique should not affect behaviour or survival. Evidence produced by Gerking (1953) suggests that this is, in fact, the case and it showed that fish adapt readily to the loss of a fin. All fish once marked were returned one by one to the region of netting. Three recaptures were made, the first, one hour after marking, the second, fifteen minutes after the first, and the third four days later. Recaptures were made at the same time of day, the importance of this will be shown in section 7.

(b) Loach - mark and recapture. The method of capture using the seine net can be considered a large scale version of that used by Smyly (1955), and is determined by the behaviour of the fish which remains dormant, settling under stones and rocks on the bed of the river during daylight hours, and becoming active at night. To catch the loach, Smyly used a hand net with a D shaped mouth, the straight side of the D lying on the bottom. In running water the net was placed across the current with the mouth of the net facing upstream. Stones immediately above the net were turned over by kicking vigorously and after a few moments the net lifted and fish removed. In this study a seine net was employed instead
of a hand net, the movement of the leads over small stones and rocks being enough to disturb the loach and render them liable to capture. For each capture date, four sweeps of the net were made over the study area of 175 square metres. Netting was always carried out in an upstream direction. Lengths of the fish were recorded on waxed graph paper. Fish were replaced in the centre of the study area after marking.

In mark recapture studies, to estimate population numbers, the proportion of marked fish appearing in a random sample provides an estimate of the fish in the total population. The inadequacy of this method for these studies will be discussed in the conclusion. The method can be expressed mathematically as follows:

\[ N = \frac{mc}{r} \]

where \( N \) = total number of fish in the population
\( m \) = total number of marked fish in the population
\( c \) = number of fish in the sample
\( r \) = number of marked fish recaptured in the sample

The standard of error of the estimate is computed thus

\[ \text{S.E.}(N) = \sqrt{\frac{(N-m)(N-c)}{mc(N-1)}} \]

(ii) Results: (a) Minnow Phoxinus phoxinus (L)

<table>
<thead>
<tr>
<th>Time</th>
<th>Sample</th>
<th>Number of marked fish</th>
<th>Catch</th>
<th>Recaptures</th>
<th>Number dead or injured on capture</th>
<th>Unmarked catch</th>
<th>Estimate of ( N )</th>
<th>Area covered</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 hrs.</td>
<td>Sample 1</td>
<td>373</td>
<td>56</td>
<td>28</td>
<td>0</td>
<td>28</td>
<td>746 ± 138 S.E.</td>
<td>40 sq. m. 18.65/m²</td>
</tr>
</tbody>
</table>
+1.25 hrs. Sample 3
Catch = 56
Recaptures = 20
Number dead or injured on capture = 0
Unmarked catch = 36
Estimate of N = 1044 ± 310 S.E.
Area covered = 40 sq.m. = 26.1/m²

+96 hrs. Sample 4
Catch = 80
Recapture = 2
Number dead or injured on capture = 0
Unmarked catch = 78
Estimate of N = 14920 ± S.E. = 4 x 14,920

This latter estimate is unreliable and is due to an insufficient number of marked fish present within the total population for the area i.e. immigration and emigration had occurred.

(b) Stone Loach. Noemacheilus barbatulus (L)
0 hrs. Sample 1
Number of marked fish* = 60
* left pelvic fin cut

+24 hrs. Sample 2
Catch = 123
Recapture = 3
Number of marked fish* = 123
* right pelvic fin cut
Total number of marked fish* = 180
Unmarked catch = 120
Estimate of N = 2460 ± S.E. 1368
Area covered = 175 sq.m. = 14.1/m²
+96 hrs. Sample 2

<table>
<thead>
<tr>
<th>Catch</th>
<th>= 61</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recapture</td>
<td>= 7 (2 marked - left pelvic) (5 marked - right pelvic)</td>
</tr>
<tr>
<td>Number dead or injured on capture</td>
<td>= 0</td>
</tr>
<tr>
<td>Unmarked catch</td>
<td>= 54</td>
</tr>
<tr>
<td>Estimate of N</td>
<td>= 1501 ± S.E. 630</td>
</tr>
<tr>
<td>Area covered</td>
<td>= 175 sq.m. = 8.6/m²</td>
</tr>
</tbody>
</table>

(iii) Conclusions: It is thought that the results provide a reliable estimate for the stone loach population in the area and the two initial estimates obtained for the minnows of 18.65/m² and 26.1/m² give an indication of the numbers of minnows shoaling in the area at the time of capture. The third estimate may provide an estimate for the total minnow population in the area, though no true reliance can be laid on its accuracy owing to the high standard error value obtained.

Mark and recapture studies require that (a) no immigration or emigration occurs (b) the animal is no more liable to capture once marked (c) the behaviour of the animal is in no way impaired. It is unlikely that (a) applied for the third population estimate of the minnow, for owing to shoal movements both into and out of the study area, it is likely that a considerable degree of dispersal had taken place during this period. The best estimates of density are obtained when the proportion of recaptures in the census is high and the area occupied by marked fish is reliably known. As will be shown in section 7 this method does not mark a representative sample of the minnow population but only a representative sample of the number of minnows shoaling in the study area. Mann (1971) reported a similar difficulty with minnow populations in production studies. With more efficient capture methods, involving the netting off of sections of river, and a more efficient marking method e.g. subcutaneous injection (Ricker 1968) or
immersion staining (Matthews 1970), a more reliable estimate of numbers in the area could have been made. Time, and lack of equipment and aid, did not, however, permit this.

Estimates of numbers shoaling in the area are in the range 750-1050 which if evenly dispersed over the netting area give values of 18-26 fish per m². This exercise was carried out late in the spawning period, when numbers present in the area were lower than at earlier times during the spawning period. Using better capture and marking methods as outlined above, investigations on the population during the spawning period could be made, together with studies on the sex ratio variance exhibited in this study and discussed in section 5. Estimates of population numbers would not include juvenile fish or any other segment of the population absent from the area, but would give a negatively biased estimate as do the figures shown above.

Population numbers obtained for the stone loach are a satisfactory estimate for the area studied, at the time of capture. Estimates for larger sections of the river can only be obtained using more elaborate methods. Vastly different estimates would have been obtained at night, for as will be described under section 7, large numbers of loach move into the shallow sandy regions of the river after dusk, having remained hidden during the day under stones in the faster flowing areas of the river. Stone loach move into these areas at night in order to feed. Stomach content analysis of stone loach sampled during different periods of the day confirm this.
7. **Daily activity of minnow shoals**

(i) **Methods:** Seine netting was undertaken over a twenty-four hour period during late August, after spawning, at the Croxdale site. One sweep of the net was made every four hours during the daily cycle, over the same stretch of river. The depth of the river at this point was 30-50 cms.

Times were as follows:

1. 1600 hrs.  
2. 2000 hrs.  
3. 2400 hrs.  
4. 0400 hrs.  
5. 0800 hrs.  
6. 1200 hrs.

All fish netted for each period were counted. For samples 1 and 6 a subsample was obtained (method as P.31) for length measurement, owing to the size of the sample. Samples 2, 3, 4 and 5 represent actual numbers netted. Fish lengths were measured pricking out onto waxed graph paper. Fork length of the fish was taken measuring from the anteriormost extremity of the fish to the tip of the median rays of the tail. All fish after measurement were returned to the river in the netting region.

(ii) **Results:** Results of the netting are presented in histogram form. (Fig. 16)

Numbers of fish netted for each period are as follows.

1. 420
2. 34
3. 62
4. 94
5. 0
6. 1114

Figures indicate a movement of shoals of different size classes of fish,
into and out of the netting area during the twenty-four hour period. The movements exhibited occur at different periods for different sections of the population. At 1200 and 1600 hours the population in the area is represented by large shoals of two size classes, young first year fish and one year old fish (0+, I+). The 2000 hours netting shows an absence of the one year old fish. Movement is inferred from presence or absence. Results for the 2400 hours and 0400 hours periods are marked by the absence of 0+ fish and presence of fish of I+ and II+ age groups. Large numbers of stone loach (Noemacheilus barbatulus (L)) were netted in these latter samples. Evidently a movement of loach occurs over the same period as the movement of the larger minnows.

(iii) Conclusions:— Results would seem to suggest movements of minnow shoals based on diel changes in light intensity. The larger members of the population, I+ and II+ year fish move into the shallow water areas at dusk whilst 0+ fish are absent from the shallow water areas during this overnight period. John (1959) describes late evening movements of larger chub (Gila atraria L) into shallow water areas to feed, with a corresponding movement of younger fish into deeper water. In the minnow, movement of the young fish may either have been (1) into the mainstream or (2) into deeper slack water downstream of the study area. The latter possibility would appear to be the more likely explanation, though a more intensive netting programme should be attempted to clarify the situation. The segregation in the movements of the younger and older fish, it is suggested, could be a factor in reducing predation on younger fish by larger fish. No reports are available of predation of larger minnows on young minnows, though Berwein (1941) describes aggressive behaviour exhibited between shoals of larger minnows, and individuals and shoals of young minnows.
Differences other than presence or absence could have affected the number caught. During daylight hours, the fish may see the net more easily and therefore tend to avoid it. Visual observation prior to netting during the day and the absence of O+ year fish in the night catch indicate the unlikeness of this possibility.

The degree of movement into shallow waters by O+ and I+ fish is probably dependent on light intensity, with shoals present in less depth of water on days of high light intensity, as compared with those days showing a reduced light intensity. Harden-Jones (1956) reports a complete disregard for high light intensities during the spawning period, a point which could explain the different sampling results obtained for the 2000 hour period in section 5, as compared with the results obtained for this section. I+ year fish move out of the area earlier in the evening than do O+ year fish probably due to an earlier response to reduction in light intensity. Different responses have previously been shown for these different size classes in relation to disturbances (see section 3 (ii) (f) The 'fright reaction'.) Return of the I+ year fish occurs after dusk, though much smaller numbers were present. Dispersal of the larger shoals had probably occurred. It is unsure whether the representatives of the I+ year class present during daylight hours are the same as those present in the night catches. Marking of the fish after each netting would have helped in this respect.

A segregation in shoal movements might also act as a method of decreasing the unfavourable effects of high population density on production, thus reducing competition, lowering the mortality rate and increasing the growth rate. The relationship between migration and movements and production in freshwater fish has been well reviewed by Northcote (1967).

Shoal movements to and from the shallow area probably occur at dawn and dusk, times when the effectiveness of predators is reduced.
Hasler and Villemonte (1953) reported a pre-sundown movement of shoals of perch (*Perca flavescens* L) from 25'-35' depths where they are present during daylight hours, into shallow waters of 18'-30' depth. They postulated that with the reduction in light intensity, the perch lose their tendency to shoal, settling to the bottom and maintaining contact with the sand. Similar movements from deep to shallow water appear to be shown by the larger minnows and stone loach, though probably for different reasons, for the loach is an active night feeder. A nocturnal quiescent behaviour shown by the minnow could have survival value in escaping natural enemies. During inshore movements of minnow at dusk, feeding activity was often observed. A high proportion of fish examined at this time (see section 3 (ii) (e)) showed relatively full guts. It is unlikely that minnows feed to any large extent overnight. Guts examined during morning hours showed few contents.

**SIMPLIFIED MODEL OF MOVEMENTS DURING THE 24 HOUR PERIOD**
SUMMARY

1. Behavioural observations were made on minnow shoals in the River Wear and River Browney, County Durham. Three adaptive features are suggested for shoaling behaviour, with evidence to support these ideas:
   (a) during the breeding season shoaling plays an important part in the reproductive activities of the species.
   (b) Shoaling is an important factor in the location of locally abundant food.
   (c) Shoaling affords a certain degree of protection against predation.

2. Experimental and behavioural observations in the laboratory indicate the importance of the visual sense in shoaling behaviour. Aspects of the 'fright reaction' are discussed.

3. Routine netting was carried out at two sites on the River Wear in an attempt to investigate the population structure over a period of time. Length frequency histograms indicate a stable population structure over the netting period though the proportion of larger minnows (5.6cm+) present shows variation with time and site. A significant variation in the sex ratio within the sample is shown on three occasions. Length-weight regression equations are presented for the sampling period.

4. Mark and recapture studies were undertaken on minnow and stone loach populations at Croxdale site. The accuracy of these methods in relation to both species is criticised.

5. Seine netting was performed at Croxdale site every four hours over a twenty-four hour period in order to investigate diel shoal movements. Suggestions are put forward to explain the movements which are probably triggered by several factors including changes in light intensity.


ACKNOWLEDGEMENTS

Gratitude is due to the Northumbrian River Authority for permission to carry out the project on the River Wear, County Durham. I also wish to express my thanks to Ferryhill Angling Club and the Royal Ordnance Factory, Birtley Angling Club in allowing me to net within their stretches of the river. Thanks are also due to Mr. W. B. Woodward for help and encouragement during the project and to Mr. P. J. Fox B.Sc. and Mr. B. Brenkley for their help with netting.
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6(b) POD FORMATION IN PHOXINUS PHOXINUS (L)
Fig. 2. CROXDALE SITE.
Fig. 3. FINCHALE PRIORY SITE.
**Chironomid larvae**

**Chironomid pupae**

**Chironomid adults**

**Ephemeroptera nymphs**

**Ephemeroptera adults**

**Trichoptera larvae**

**Eggs (Pisces)**

**Plecoptera nymphs**

**Coleoptera**

**Hydracarina**

**Hymenoptera (Terrestrial)**

**Diptera (adult)**

**Diptera (larvae)**

**Diptera (pupae)**

**Crustacea**

**Algae**

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**FISH LENGTH KEY**

- A = 2.1–4.0 cms.
- B = 4.1–6.0 cms.
- C = 6.1+ cms.

---

**Fig. 4 STOMACH CONTENT ANALYSIS BY % POINTS**

FINCHEALE PRIORY

15-6-72 2000–2100 hrs.
FIG. 5 LENGTH-FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS (L)
(1) CROXDALE 17.5.72 1900-2100 HRS.
FIG. 6  LENGTH-FREQUENCY DISTRIBUTION OF THOXINUS THOXINUS (L)
(2) CROXDALE 21.6.72  2000-2100 HRS

NUMBER OF FISH

20

18

16

14

12

10

8

6

4

2

0

LENGTH cms

2.0

3.0

4.0

5.0

6.0

7.0

8.0
FIG. 7 LENGTH-FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS (L.
(3) CROXDALE 28.6.72  2000-2100 HRS
FIG. 8 LENGTH- FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS (L)
(4) CHOIXDALE 5.7.72 2000-2100 HRS

NUMBER OF FISH

LENGTH cm

2.5
3.5
4.5
5.5
6.5
7.5
FIG. 9 LENGTH-FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS (L)
(5) CHIDALE 12.7.72 2000-2100 HRS
Fig. 10 LENGTH-FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS (L)
(1) PINCHALE PRIORY 22.5.72 1900-2130 HRS
FIG. 12 LENGTH-FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS (L)
(3) FINCHALE FRIARY 23.6.72 2000-2100 HRS
FIG. 13 LENGTH-FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS
(4) FINCHALE PRIORY 29.6.72 2000-2130 HRS
FIG. 14 LENGTH-FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS (L)
(5) FINCHALE, PRIORY 7.7.72 2000-2130 HRS
FIG. 15 LENGTH-FREQUENCY DISTRIBUTION OF PHOXINUS PHOXINUS (L)
(6) PINCHALE PRIORY 14.7.72 2000-2130 HRS.
<table>
<thead>
<tr>
<th>FOOD TYPE</th>
<th>LENGTH OF FISH</th>
<th>2.1 - 4.0 cms.</th>
<th>4.1 - 6.0 cms.</th>
<th>6.1 cms. +</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% POINTS</td>
<td>OCCURRENCE</td>
<td>% POINTS</td>
<td>OCCURRENCE</td>
</tr>
<tr>
<td>CHIRONOMID LARVAE</td>
<td>66.97</td>
<td>52.0</td>
<td>48.4</td>
<td>33.5</td>
</tr>
<tr>
<td>CHIRONOMID PUPAE</td>
<td>0.53</td>
<td>1.55</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CHIRONOMID ADULTS</td>
<td>21.1</td>
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<td>17.3</td>
<td>20.62</td>
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<td>EPHEMEROPTERA NYMPHS</td>
<td>6.06</td>
<td>12.0</td>
<td>14.4</td>
<td>20.62</td>
</tr>
<tr>
<td>EPHEMEROPTERA ADULTS</td>
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<td>1.55</td>
<td></td>
<td></td>
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<td>4.0</td>
<td>5.1</td>
<td>6.70</td>
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<td>0.52</td>
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<td>PLECOPTERA NYMPHS</td>
<td>0.23</td>
<td>1.04</td>
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<td>0.52</td>
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<td></td>
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<tr>
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<td>0.92</td>
<td>4.0</td>
<td>0.05</td>
<td>0.52</td>
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<td>HYMENOPTERA (terrestrial)</td>
<td>0.69</td>
<td>0.52</td>
<td>5.68</td>
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<tr>
<td>DIPTERA LARVAE</td>
<td>1.85</td>
<td>0.52</td>
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</tr>
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<td>DIPTERA PUPAE</td>
<td>18.18</td>
<td>7.7</td>
<td></td>
<td></td>
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<tr>
<td>DIPTERA ADULTS</td>
<td>5.55</td>
<td>4.12</td>
<td>23.86</td>
<td>23.1</td>
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<tr>
<td>CRUSTACEA</td>
<td>0.21</td>
<td>1.04</td>
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<td>ALGAE</td>
<td>3.67</td>
<td>8.0</td>
<td>1.8</td>
<td>5.61</td>
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<td>7.7</td>
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**TABLE 1 GUT CONTENT ANALYSIS (see p.11)**
<table>
<thead>
<tr>
<th>DATE</th>
<th>1. CROXDALE SITE</th>
<th>DATE</th>
<th>2. FINCHALE PRIORY</th>
</tr>
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<tbody>
<tr>
<td>17.5.72</td>
<td>N = 78</td>
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</tr>
<tr>
<td></td>
<td>F = 39</td>
<td></td>
<td>F = 37</td>
</tr>
<tr>
<td></td>
<td>$\chi^2 = 0$</td>
<td></td>
<td>$\chi^2 = 2.844$</td>
</tr>
<tr>
<td></td>
<td>N.S.</td>
<td></td>
<td>N.S.</td>
</tr>
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<td>N = 114</td>
<td>15.6.72</td>
<td>N = 192</td>
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<td></td>
<td>M = 50</td>
<td></td>
<td>M = 92</td>
</tr>
<tr>
<td></td>
<td>F = 64</td>
<td></td>
<td>F = 100</td>
</tr>
<tr>
<td></td>
<td>$\chi^2 = 1.263$</td>
<td></td>
<td>$\chi^2 = 0.3332$</td>
</tr>
<tr>
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<td>N.S.</td>
<td></td>
<td>N.S.</td>
</tr>
<tr>
<td>21.6.72</td>
<td>N = 394</td>
<td>23.6.72</td>
<td>N = 296</td>
</tr>
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<td></td>
<td>M = 216</td>
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<td>M = 177</td>
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<tr>
<td></td>
<td>F = 178</td>
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<td>F = 119</td>
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<td></td>
<td>$\chi^2 = 11.3648$</td>
</tr>
<tr>
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<td>N.S.</td>
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<td>N = 284</td>
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<td>N = 210</td>
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<td>M = 183</td>
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</tr>
<tr>
<td></td>
<td>F = 101</td>
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<td>$\chi^2 = 23.676$</td>
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<td>$\chi^2 = 0.2278$</td>
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<td>p &lt; .001</td>
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<td>F = 106</td>
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<td>F = 82</td>
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<td>$\chi^2 = 0.0418$</td>
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<td>$\chi^2 = 10.608$</td>
</tr>
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<td></td>
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<td>N.S.</td>
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<td></td>
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<td></td>
<td>F = 111</td>
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<td>F = 82</td>
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<td>$\chi^2 = 4.4098$</td>
<td></td>
<td>$\chi^2 = 10.608$</td>
</tr>
<tr>
<td></td>
<td>N.S.</td>
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<td>N.S.</td>
</tr>
</tbody>
</table>

$N$ = sample number

$M$ = male

$F$ = female

FISH $0+$ = young 1st year fish

**TABLE 2 WEEKLY NETTING SAMPLES.**
<table>
<thead>
<tr>
<th>CODE NUMBER</th>
<th>LENGTH (cms)</th>
<th>WEIGHT (gms)</th>
<th>SEX</th>
<th>CONDITION FACTOR k</th>
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<td>10.3</td>
<td>16.72</td>
<td>FEMALE</td>
<td>1.53</td>
</tr>
<tr>
<td>FP5/B</td>
<td>9.5</td>
<td>15.07</td>
<td>FEMALE</td>
<td>1.75</td>
</tr>
<tr>
<td>FP5/C</td>
<td>9.2</td>
<td>11.15</td>
<td>FEMALE</td>
<td>1.43</td>
</tr>
<tr>
<td>FP5/D</td>
<td>10.1</td>
<td>15.05</td>
<td>FEMALE</td>
<td>1.46</td>
</tr>
<tr>
<td>FP5/E</td>
<td>10.0</td>
<td>15.55</td>
<td>FEMALE</td>
<td>1.55</td>
</tr>
<tr>
<td>FP5/F</td>
<td>9.1</td>
<td>10.95</td>
<td>MALE</td>
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</tr>
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<td>19.339</td>
<td>FEMALE</td>
<td>1.57</td>
</tr>
<tr>
<td>FP5/H</td>
<td>8.7</td>
<td>10.545</td>
<td>FEMALE</td>
<td>1.60</td>
</tr>
<tr>
<td>FP5/J</td>
<td>10.5</td>
<td>17.110</td>
<td>FEMALE</td>
<td>1.47</td>
</tr>
<tr>
<td>FP5/K</td>
<td>8.7</td>
<td>11.265</td>
<td>FEMALE</td>
<td>1.71</td>
</tr>
<tr>
<td>FP5/L</td>
<td>9.6</td>
<td>14.274</td>
<td>FEMALE</td>
<td>1.61</td>
</tr>
<tr>
<td>FP5/M</td>
<td>10.1</td>
<td>19.942</td>
<td>FEMALE</td>
<td>1.935</td>
</tr>
<tr>
<td>FP5/N</td>
<td>9.4</td>
<td>12.766</td>
<td>FEMALE</td>
<td>1.54</td>
</tr>
<tr>
<td>FP5/O</td>
<td>10.1</td>
<td>16.160</td>
<td>FEMALE</td>
<td>1.57</td>
</tr>
<tr>
<td>FP5/P</td>
<td>8.8</td>
<td>11.02</td>
<td>FEMALE</td>
<td>1.61</td>
</tr>
<tr>
<td>FP5/Q</td>
<td>7.6</td>
<td>7.321</td>
<td>MALE</td>
<td>1.67</td>
</tr>
<tr>
<td>FP5/R</td>
<td>8.3</td>
<td>9.058</td>
<td>FEMALE</td>
<td>1.58</td>
</tr>
<tr>
<td>FP5/S</td>
<td>8.5</td>
<td>10.696</td>
<td>FEMALE</td>
<td>1.74</td>
</tr>
<tr>
<td>FP5/T</td>
<td>7.5</td>
<td>6.34</td>
<td>FEMALE</td>
<td>1.50</td>
</tr>
</tbody>
</table>

CONDITION FACTOR \( k = \frac{\text{WEIGHT IN GRAMS} \times 100}{(\text{LENGTH IN CENTIMETRES})^3} \)

**TABLE 3** SPAWNING FEMALE SHUAL

DATE 22.5.72  SITE 2  FINCHALE PRIORY TIME 2000 hrs.
<table>
<thead>
<tr>
<th>DATE</th>
<th>LENGTH AND SEX</th>
<th>REGRESSION EQUATION</th>
<th>SAMPLE</th>
<th>b significantly different from 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>17.5.72</td>
<td>0.55 mm. M</td>
<td>$y = -2.0860 + 3.1683x$</td>
<td>39</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>0.55 mm. F</td>
<td>$y = -2.0646 + 3.1692x$</td>
<td>39</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mm. M.</td>
<td></td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>56+ mm. F.</td>
<td></td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>21.6.72</td>
<td>0.55 mm. M</td>
<td>$y = -1.9763 + 3.1606x$</td>
<td>211</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>0.55 mm. F</td>
<td>$y = -1.9909 + 3.1853x$</td>
<td>174</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>56+ mm. M.</td>
<td>$y = -1.8912 + 3.0617x$</td>
<td>5</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mm. F.</td>
<td>$y = -1.9781 + 3.1849x$</td>
<td>4</td>
<td>No</td>
</tr>
<tr>
<td>28.6.72</td>
<td>0.55 mm. M</td>
<td>$y = -2.1429 + 3.4022x$</td>
<td>166</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>0.55 mm. F</td>
<td>$y = -2.1219 + 3.3621x$</td>
<td>82</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>56+ mm. M.</td>
<td>$y = -1.8520 + 2.9988x$</td>
<td>17</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mm. F.</td>
<td>$y = -1.7024 + 2.8374x$</td>
<td>19</td>
<td>No</td>
</tr>
<tr>
<td>5. 7.72</td>
<td>0.55 mm. M</td>
<td>$y = -2.0595 + 3.2676x$</td>
<td>105</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>0.55 mm. F</td>
<td>$y = -2.0553 + 3.2699x$</td>
<td>93</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>56+ mm. M.</td>
<td>$y = -0.7656 + 1.5511x$</td>
<td>4</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mm. F.</td>
<td>$y = -2.1829 + 3.4385x$</td>
<td>13</td>
<td>No</td>
</tr>
<tr>
<td>12.7.72</td>
<td>0.55 mm. M</td>
<td>$y = -2.1022 + 3.3516x$</td>
<td>78</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>0.55 mm. F</td>
<td>$y = -2.1010 + 3.3538x$</td>
<td>78</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>56+ mm. M.</td>
<td>$y = -1.7568 + 2.9004x$</td>
<td>16</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mm. F.</td>
<td>$y = -1.8539 + 3.0298x$</td>
<td>33</td>
<td>No</td>
</tr>
</tbody>
</table>

M = Male,  F = Female.

Regression equation - \( \log W = \log a + b (\log L) \)
where \( W \) = weight (gms) \( L \) = length (ems).
Statistical significance is taken at the 1% level.

**TABLE 4. CROXDALE - REGRESSION ANALYSES.**
<table>
<thead>
<tr>
<th>DATE</th>
<th>LENGTH AND SEX</th>
<th>REGRESSION EQUATION</th>
<th>SAMPLE</th>
<th>b significantly different from 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>22.5.72</td>
<td>0.55mms. M</td>
<td>( y = -2.0694 + 3.1618x )</td>
<td>53</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>0.55mms. F</td>
<td>( y = 2.0322 + 3.0930x )</td>
<td>37</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mms. M</td>
<td></td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>56+ mms. F</td>
<td></td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>15.6.72</td>
<td>0.55mms. M</td>
<td>( y = -1.8958 + 3.0404x )</td>
<td>48</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>0.55mms. F</td>
<td>( y = -2.0706 + 3.3267x )</td>
<td>52</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>56+ mms. M</td>
<td>( y = -2.7386 + 4.2308x )</td>
<td>2</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>56+ mms. F</td>
<td>( y = -1.8085 + 3.0039x )</td>
<td>12</td>
<td>No</td>
</tr>
<tr>
<td>23.6.72</td>
<td>0.55mms. M</td>
<td>( y = -1.9058 + 3.0942x )</td>
<td>86</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>0.55mms. F</td>
<td>( y = -2.1280 + 3.4292x )</td>
<td>80</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>56+ mms. M</td>
<td>( y = -1.8441 + 3.0224x )</td>
<td>6</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mms. F</td>
<td>( y = -2.1602 + 3.4512x )</td>
<td>20</td>
<td>Yes</td>
</tr>
<tr>
<td>29.6.72</td>
<td>0.55mms. M</td>
<td>( y = -2.0559 + 3.3041x )</td>
<td>156</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>0.55mms. F</td>
<td>( y = -1.9243 + 3.1193x )</td>
<td>98</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mms. M</td>
<td>( y = -1.9096 + 3.0905x )</td>
<td>21</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mms. F</td>
<td>( y = -2.0914 + 3.3227x )</td>
<td>21</td>
<td>No</td>
</tr>
<tr>
<td>7.7.72</td>
<td>0.55mms. M</td>
<td>( y = -2.0168 + 3.2486x )</td>
<td>74</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>0.55mms. F</td>
<td>( y = -1.9388 + 3.1526x )</td>
<td>60</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mms. M</td>
<td>( y = -2.1134 + 3.3695x )</td>
<td>8</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mms. F</td>
<td>( y = -1.8269 + 3.0078x )</td>
<td>16</td>
<td>No</td>
</tr>
<tr>
<td>14.7.72</td>
<td>0.55mms. M</td>
<td>( y = -2.0655 + 3.3056x )</td>
<td>108</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>0.55mms. F</td>
<td>( y = -1.9949 + 3.2120x )</td>
<td>68</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>56+ mms. M</td>
<td>( y = -1.8225 + 2.9018x )</td>
<td>20</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>56+ mms. F</td>
<td>( y = -1.9842 + 3.1842x )</td>
<td>24</td>
<td>No</td>
</tr>
</tbody>
</table>

M = Male,  F = Female.

Regression equation - \( \log W = \log a + b (\log L) \)
where \( W = \text{weight (gms)} \)  \( L = \text{length (cms)} \).

Statistical significance is taken at the 1% level.

**TABLE 5** FINCHALE PRIORY - REGRESSION ANALYSES
Fig 16 Daily movements—four-hourly samples.

LENGTH cm

N=133
1200 hours
N=0
0800 hours
N=94
0400 hours
N=62
2400 hours
N=34
2000 hours
N=155
1600 hours
Plate 1 (a) Croxdale site (upstream)
Plate 1 (b) Croxdale site (downstream)
Plate 2(a) Finchale Priory site (downstream)
Plate 2 (b) Finchale Priory site—with net in foreground
Plate 3(a) Shoal movements in *Phoxinus phoxinus* (L)
Plate 3(b) Shoal movements in *Phoxinus phoxinus* (L)
Plate 4(a) Shoal Break-up in Phoxinus phoxinus (L)
Plate 4(b) Milling Behaviour in Phoxinus phoxinus (L)
Plate 5(a) Shoal movements in *Phoxinus phoxinus* (L)
Plate 5(b) Shoal movements in *Phoxinus phoxinus* (L)
Plate 6(a) Mill formation in *Phoxinus phoxinus* (L)
Plate 6(b) Pod breakdown in *Phoxinus phoxinus* (L)
Plate 7(a) Milling behaviour in Phoxinus phoxinus (L)
Plate 7(b) Pod breakdown in Phoxinus phoxinus (L)
Plate 8(a) Surface feeding in *Phoxinus phoxinus* (L)
Plate 8(b) Pod formation in *Phoxinus phoxinus* (L)