The effects of environmental complexity upon the aggressive behavior and growth of juvenile brown trout (salmo trutta L.) and the carrying capacity of the environment

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THE EFFECTS OF ENVIRONMENTAL COMPLEXITY UPON THE AGGRESSIVE BEHAVIOUR AND GROWTH OF JUVENILE BROWN TROUT (Salmo trutta L.) AND THE CARRYING CAPACITY OF THE ENVIRONMENT

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(MSB 6008)

OFFERED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN THE DISCIPLINE OF ZOOLOGY

1st JULY, 1976
Best Copy Available
STATEMENT

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ABSTRACT

Experiments were performed in stream tanks and aquaria to investigate the effects of environmental complexity upon the aggressive behaviour and growth of juvenile brown trout (Salmo trutta L.) and the carrying capacity of the environment. Natural materials and various structures were used to provide environmental complexity.

Aggressive interactions were found to be significantly more frequent in simple environments than in complex ones. The different types of structures used to modify the complexity of the experimental environments had different effects upon the observed levels of aggressive behaviour; structures providing overhead cover were associated with the lowest levels of aggression. Increasing fish density resulted in relatively greater increases in aggression in simple environments.

The wigwag display of the fish was analysed and found to be a highly ritualised, defensive manoeuvre, the efficiency of which was determined by the social ranks of the fish involved.

Carrying capacity of complex environments was significantly greater than that of simple environments. There was a significant inverse correlation between aggression and resident population size in the environment types used.

In the growth experiment, different relationships between individual fish's specific growth rates and their size rank position were found in populations of fish kept in simple and complex environments. The differences were probably associated with the different levels of aggression observed in the two environment types and the effect of environmental complexity upon feeding behaviour.
ACKNOWLEDGEMENTS

I wish to thank Dr. M.C. Varley for her encouragement, advice and criticism during my research.

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1. EXPERIMENTS ON THE EFFECT OF ENVIRONMENTAL COMPLEXITY UPON AGGRESSIVE BEHAVIOUR OF JUVENILE BROWN TROUT
1.1

Introduction

Aggressive behaviour has been widely observed in fish and falls into two main categories: aggression associated with spawning and non-reproductive aggression.

Some species of fish exhibit aggressive behaviour during the breeding season only; others do so throughout the year. Fish which are aggressive only when breeding are usually regarded as 'shoal fish' for the rest of the year, and notable examples are the Stickleback, Gasterosteus aculeatus, (Van Den Assem 1967) and the bream, Abramis brama, (Fabricius, 1951). This sort of aggressive behaviour is usually associated with territoriality and is often restricted to males. The control of breeding aggression is often hormonal and its appearance is timed by the effects of environmental parameters, especially day length, upon the endocrine system.

Non-spawning aggressive behaviour occurs in both adults and juveniles of many species, for example burbot, Lota lota, (Fabricius, 1955) char, Salmo alpinus, (Fabricius, 1952 and 1954) grayling, Thymallus.

ERRATUM

Page 1 (Fabricius, 1952 and 1954)

should read (Fabricius, 1952 and Fabricius and Gustafson, 1954)

Salmo gairdneri kamloops, and suggested that the decline in aggression in spring (March - April) may have been the result of increasing light
or temperature. In the same paper the limiting effect of light intensity upon the frequency of aggression was demonstrated and it was suggested that the decrease in aggression with decreasing light was associated with the tendency of salmonids to sink to the bottom and remain inactive at night (eg. coho salmon, *Oncorhynchus kisutch*, Hoar, 1953).

Water velocity is an important factor affecting territory maintenance in salmonids but aggression persists when velocity is too low for territoriality. This has been observed in Atlantic salmon, *Salmo salar*, by Kalleberg (1958) and is supported by the circumstantial evidence that several studies on aggressive behaviour in salmon and trout have been performed in still-water aquaria (Newman, H.W., 1959; Newman, M.A., 1956).

The density of fish in a population also influences aggressive behaviour. This has been shown for juvenile Atlantic salmon by Keenleyside and Yamamoto (1962) who demonstrated that, with increasing fish density, the rate of aggression, measured as the number of nips per fish per hour, increased to a certain density and thereafter declined. The same authors also demonstrated the short-term effects of feeding upon rate of aggression. Availability of food can also have more long-term effects upon aggressive behaviour, as was shown for Atlantic salmon by Symons (1963) who found that aggressive behaviour increased and social hierarchies were strengthened when the fish were starved.

There is some evidence that aggression and territoriality may be affected by hormonal factors as Hoar (1953) described the disappearance of territorial behaviour during the parr-smolt transformation of coho salmon.

The physical configuration of the environment of fish has been shown to affect their territorial and aggressive behaviour. In the case of
spawning territories it is known that the topography of the spawning area can affect the size of the territory (Fabricius, 1951). For coho salmon and steelhead trout (*Salmo gairdneri*) aggression in juvenile fish was found to be higher in riffle than pool environments (Hartman, 1965).

Hartman (1963) tested the effect of adding various structures to the environment of juvenile brown trout. He found that reaction to the structures varied from winter to spring but stated that the "...amount and type of aggressive behaviour was unaffected by the type of structure used to modify the floors of the tank.". However, the relevant data were not presented, and neither was it stated whether or not there was any difference in the amount or type of aggression between control groups and groups of fish in tanks with structures.

That the type of structure should have no effect upon aggressive behaviour appears illogical in view of the relationship between the complexity of a stream bed and the size of salmonid territories. Kalleberg (1958) demonstrated that territory size in juvenile Atlantic salmon was reduced when large stones, representing an increase in the complexity of the stream bed, were added to the environment. Similar observations on rainbow trout were made in natural conditions by Yamagishi (1962). Both of these authors ascribed the cause of this phenomenon to visual isolation resulting from the complex environment. (See also Stuart, 1953). If it is accepted that increase in environmental complexity brings about decreased territory size, then it follows that complexity must also influence aggressive behaviour, as it is the mechanism by which territories are maintained.

In the instances given above, (Kalleberg 1958 and Yamagishi 1962) reduction in territory size was associated with increased population density and aggression per unit area of environment may have increased
with environmental complexity. The present investigation was carried out primarily to examine the effects of environmental complexity upon aggressive behaviour of juvenile brown trout in situations where the population size was fixed, by comparing aggressive behaviour in environments of different or changing complexity. In addition, one experiment was performed to compare aggressive behaviour in environments contrasting in complexity and containing varying densities of fish.
Description of Aggressive Behaviour in Juvenile Brown Trout

Aggressive behaviour has been recorded in many salmonid species and is well documented (Kelleberg, 1953, Atlantic salmon and brown trout; Newman, 1956, brook trout (Salvelinus fontinalis) and rainbow trout; Stringer and Hoar, 1955, Kamloops trout; Fabricius, 1952, char; Hartman, 1965, coho salmon and steelhead trout; Jenkins, 1959, brown and rainbow trout). The various components of aggressive behaviour do not differ greatly among species and interspecific aggression is frequently seen, for example between brook and rainbow trout (Newman 1956).

Brown trout have a typical repertoire of aggressive behaviour, including ritualised displays as well as actual fighting. In the present investigation six individual components were recognised, viz; Lateral and Frontal Threat, Nip, Chase, Submissive display and Wigwag display.

In all experiments, the same components of aggressive behaviour were recognised. To avoid reiteration at the beginning of each experiment the behavioural components are described below.

1.2.1

Lateral Threat  The lateral threat was a display characterised by erection of the fins and stiffening of the body. The extent to which the fins were raised depended upon the intensity of the display but in all cases the fins were clearly extended. Another feature of the lateral threat was a slightly upwardly concave longitudinal axis of the body.

The mouth of a fish performing a lateral threat was usually closed or only slightly open but the floor of the mouth was invariably distended downwards, with the operculae slightly extended.

5
Duration of the lateral threats varied but averaged approximately 1.5 - 2.5 seconds. In the final experiment of the investigation (Third carrying capacity experiment, Section 2.4) it was noticed that the much smaller fish often performed this display for up to five seconds.

Kelleberg (1959) allocated a mainly defensive character to the lateral threat but Jenkins (1969) concluded that the display was used in offence as well as defence. In the present experiments the observations supported the view of Jenkins, especially in the case of dominant fish which frequently used the lateral threat in an offensive context.

Mutual lateral threats were seen quite often, usually between subordinate fish and, on one occasion, three fish were observed to perform this display in concert.

1.2.2

Frontal Threat Frontal threat displays were much more overtly aggressive than lateral threats. In the frontal threat the paired median fins were typically extended but the dorsal fin was usually compressed and the anal fin neither fully extended nor especially compressed. The axis of the body was arched in the opposite direction to that seen in the lateral threat with the head and tail pointing downwards.

The mouth was always opened wide in the frontal threat and the operculae were distended.

Frontal threats were usually less than one and rarely more than 1.5 seconds in duration. In context, frontal threats were always offensive and mutual frontal threats were never observed.
Nips were the most frequently observed aggressive component and took place when one fish bit another. In the majority of nips observed there was definite contact between the jaws of the attacking fish and the body of the recipient. The 'threat-nips' observed by Hartman (1965) were not seen. Nips which missed the intended target appeared to do so because the recipient fish had moved quickly enough to avoid the attack.

In coho salmon nips are usually directed towards the wrist of the tail of the attacked fish (Hoar, 1951) but in brown trout the nips appeared to be aimed mainly at the area above the lateral line between the dorsal fin and the shoulder of the fish, although nips were often aimed at the head or tail. Jones and Bell (1954) recorded the same sort of behaviour in spawning brown trout. Similar data has been reported for Kamloops trout (Stringer and Hoar, 1955).

Physical damage was often inflicted upon the fish which were nipped. Such damage took place mainly at the beginning of experiments when the aggressive behaviour was particularly violent, perhaps because of the establishment of dominance hierarchies. The commonest type of damage observed was the loss of scales, usually from the shoulder. As many as 18 scales were counted suspended in the water after a single aggressive interaction.

Another form of damage occurred when the attacking fish caught hold of one of the fins of the recipient, followed by a brief but vigorous shaking action similar to the 'prey-shaking' described by Kalleberg, 1959. A pectoral was most often gripped in this way but occasionally one of the pelvic fins was seized and in one instance the tail. After such an incident the fin which had been seized was often badly lacerated. Holding-on to fins has also been observed by Kalleberg.
(1959) in brown trout and by Newman (1956) in brook and rainbow trout. Whenever fins were seized in the way described it was by no means clear whether it was by design or accident but the shaking action of the attacking fish appeared to be directed more towards removing the fin from the attacker's mouth than to intimidation of the attacked fish, as it was performed with the mouth open.

1.2.4 Chase

Chasing was another common component of aggressive behaviour. It was usually associated with a nip or threat. When one fish nipped another which fled the flight reaction of the nipped fish appeared to stimulate the attacking fish to chase its opponent. During the actual chase the pursuing fish often performed a frontal threat or nip. Either of these activities had the effect of slowing down the pursuing fish, often allowing the chased fish to escape. In a prolonged chase the fish attempting to escape would swim at a constant speed but the pursuing fish would progress in short bursts of high speed interrupted by pauses to threaten or nip whenever the escaping fish was overtaken.

With the larger fish used, chases commonly lasted for up to nine seconds with the two fish covering the length of the tank several times, a total distance of about 8 - 8.5m.

1.2.5 Submission

Jenkins (1969) describes flight as a submissive act but in this investigation submission was recognised when a fish, invariably a subordinate, responded to a frontal or lateral threat by another fish by compressing all of its fins and sinking motionless, to the bottom of the tank.
Similar submission without flight has been described for coho salmon (Chapman, 1962) and for brook and rainbow trout (Newman, 1956).

1.2.6

**Newman** This display was observed consistently in only one experiment and contributed a very small proportion of the total aggression. However, as the descriptions of this display in the literature (Jenkins 1969, Hartman, 1965) were made in one case on a different species and in the other in a different set of environmental conditions, it was decided to attempt an analysis of this behaviour pattern. The analysis is presented at the end of BE3.

The ways in which aggression was recorded varied according to the object of the experiment. In BE2, for example, individual components were recorded for dominant and subordinate fish. In other experiments a measure of the total aggression in groups of fish was obtained by counting the number of aggressive acts during a set time.

An aggressive act was defined as an interaction between two fish involving the performance of at least one of the components of aggressive behaviour described above. To illustrate this definition, an aggressive act might be composed of a frontal threat by one fish and a submissive display, or flight by the other. A mutual lateral threat was counted as a single aggressive act. One fish chasing another was counted as a single act irrespective of the length of the chase but if the chasing was interspersed with nips or threats, each of these was counted as a separate aggressive act.

Aggressive acts most often occurred singly and were completed in a short space of time, i.e. 1 - 1.5 seconds but it was not rare to see several acts strung together in a relatively prolonged 'fight' between two individuals. Fights occurred either at the beginning of the
experiment before the hierarchy had been established or later on between subordinate fish of apparently equal social rank. The duration of fights varied but averaged about five seconds.
1.3

Behaviour Experiment 1. (BE1)

1.3.1

Objectives This experiment was carried out to determine whether or not the physical environment of juvenile brown trout affected its aggressive behaviour. Because of its preliminary nature, this experiment was designed to provide a comparison of behaviour in two extreme types of environment.

1.3.2

Materials and Methods Specifications of the tanks used in this experiment are given in section 2 of the Appendix. The tanks were designed to represent extreme types of environment, designated as Artificial and Natural. The Artificial tank was totally bare, two long walls and the bottom of glass and the end walls of P.V.C. The Natural tank was provided with a bottom of coarse gravel, varying from 1.5 to 0.0cm in depth. Larger stones were placed on the gravel and two clumps of moss were planted. Because of the relatively slow flow of water, conditions in the Natural tank represented a pool rather than riffle environment.

Fish between 6 and 9cm in length were used in groups of six. Five groups were used in each tank. The same procedure was followed with each group. When a group was introduced to a tank it was allowed to 'settle in' for a period of four days before behavioural observations were begun. During this period the fish were observed in order to allow identification of individuals and peculiarities in fin shape, opercular size or pigmentation were noted. The fish were not marked in any way but were allocated numbers, from one to six in one tank and from seven to twelve in the other. Recognition of fish was easier than anticipated.
When the settling in period was over, it was assumed that the social relations of the group of fish were stable and would not alter appreciably over the remainder of the experiment. Each group of fish was observed for five half-hour periods spaced over a total of two and a half days with one a.m. observation and one p.m. observation per whole day. Every half-hour observation followed the same pattern. The fish were fed a small amount of pelleted trout food and observation was begun ten minutes after feeding. During the half-hour, aggression of individual fish was recorded on a grid chart. Immediately following the half-hour a record was made of the amount of movement of the fish over ten minutes. Movement was recorded as the number of times vertical lines, 10cm apart, on the front of the tanks, were passed. Each complete observation on one tank took fifty minutes. All times were measured with a stopwatch.

After the five observations were completed the groups of fish were transferred to a separate stock tank, and new groups were introduced after the tanks had been cleaned. On two occasions the groups were transferred to the other experimental tank, left for four days and observed in their new environment. The data of these groups were kept separate from the main results but served as a useful check on their validity.

1.3.3

Results  a) Aggression: Table 1.1 shows the results of the five experimental runs. Aggression is expressed as the number of aggressive acts per fish per hour for each group of fish and is no indication of any within-group dominance hierarchy. There was a considerable between-group range of aggressive behaviour in each environment type but there was significantly (P = 5.0%) more aggression in the Artificial environment.
<table>
<thead>
<tr>
<th>Group Number</th>
<th>No. of aggressive acts per fish per hour in an artificial environment</th>
<th>Group Number</th>
<th>No. of aggressive acts per fish per hour in a natural environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>36.4</td>
<td>2</td>
<td>5.9</td>
</tr>
<tr>
<td>3</td>
<td>35.0</td>
<td>4</td>
<td>15.3</td>
</tr>
<tr>
<td>5</td>
<td>86.8</td>
<td>6</td>
<td>29.1</td>
</tr>
<tr>
<td>7</td>
<td>71.3</td>
<td>8</td>
<td>20.7</td>
</tr>
<tr>
<td>9</td>
<td>53.6</td>
<td>10</td>
<td>26.7</td>
</tr>
<tr>
<td>Mean</td>
<td>56.6</td>
<td>Mean</td>
<td>19.5</td>
</tr>
</tbody>
</table>
Aggressive behaviour was very similar in both environment types and chasing, nipping, frontal and lateral threats were repeatedly observed. Apart from the frequency of aggressive interactions, the most noticeable difference between the Natural and Artificial environments was the distance from which fish were attacked in the Artificial environment. Often, the attacking fish, usually the dominant individual, would swim the length of the tank (approximately 80cm) in order to nip a particular subordinate. Frequently, two or three other subordinates were passed at close range by the dominant and ignored in the pursuit of one individual. In the Natural environment aggressive interactions were, in the majority of cases, elicited by a subordinate fish approaching the dominant, rather than vice-versa. Distance between fish in the Natural environment was typically less than 30cm before aggression took place.

b) Dominance: Although the frequency of aggressive interactions differed between environments, similar social structuring was seen in all groups of fish studied. In each group of fish, individuals were allocated ranks according to what proportion of aggressive interactions they had 'won', i.e. the number of times they attacked other fish compared to the number of times they were attacked. Fish scoring 70% or more victories were classed as dominants, those scoring between 50 and 70% as subdominants and those scoring less than 50% as subordinates.

All groups of fish contained one dominant individual. There was a difference in the number of groups with subdominants. In the Artificial environment four groups contained subdominants, compared to only one group in the Natural environment.

In three of the groups in the Artificial environment it was observed that the subordinate fish kept in a tight huddle, usually positioned in one of the upper corners of the tank. Subordinate huddles were
usually formed by the end of the 'settling-in' period. Within the huddle there was very little inter-subordinate aggression. Subordinate fish in the Natural environment were rarely seen to huddle but usually lay on the bottom of the tank, close to a stone or underneath moss.

c) Movements: Activity of the fish was also affected by the topography of the environment. Although the method used to monitor activity was rather crude, differences between the two environment-types is clearly evident from Table 1.2.

d) Results of the Changed-Environment Fish: The four groups of fish involved in this part of the experiment were Nos. 1, 2, 5 and 6.

Table 1.3 shows the levels of aggression in each group before and after changing environments. Although only four groups of fish were used it is apparent that the Natural environment was associated with reduced aggression. These results support the suggestion that the observed differences in aggression between environments were caused by the environment type rather than by between-group variation in aggression.

Dominance hierarchies were not influenced by changing environments.

1.3.4

Discussion Aggressive behaviour of trout in the two environmental types differed considerably. The difference lay not in the nature of the behaviour, for the components were the same in both environments, but in the frequency with which the components were performed. For the total numbers of aggressive acts recorded, the ratio of Artificial:Natural environments was 3:1. This was similar to the ratio for activity, which was approximately 2.5:1. Whether there was more aggression in Artificial environments because there was more activity, or vice-versa, was not apparent.
TABLE 1.2
Numbers of Movements Per Fish Per Hour in Two Environment Types

<table>
<thead>
<tr>
<th>Group Number</th>
<th>Movements per fish per hour in an artificial environment</th>
<th>Group Number</th>
<th>Movements per fish per hour in a natural environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>561.6</td>
<td>6</td>
<td>175.4</td>
</tr>
<tr>
<td>7</td>
<td>411.4</td>
<td>8</td>
<td>209.0</td>
</tr>
<tr>
<td>9</td>
<td>282.8</td>
<td>10</td>
<td>177.0</td>
</tr>
<tr>
<td>Mean</td>
<td>418.6</td>
<td>Mean</td>
<td>186.8</td>
</tr>
<tr>
<td>Group Number</td>
<td>No. of aggressive acts per fish per hour in an artificial environment</td>
<td>No. of aggressive acts per fish per hour in a natural environment</td>
<td></td>
</tr>
<tr>
<td>--------------</td>
<td>-------------------------------------------------</td>
<td>-------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>36.4</td>
<td>11.6</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>42.2</td>
<td>5.9</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>86.8</td>
<td>44.6</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>49.6</td>
<td>29.1</td>
<td></td>
</tr>
</tbody>
</table>
In all groups of fish the dominant individuals were responsible for a large proportion of the total observed aggression. It seems likely, therefore, that the way in which the complexity of the environment affects the total aggression of a group of fish reflects the effect upon the behaviour of the dominant fish.
Behaviour Experiment 2. (BE2)

1.4.1

Objectives The number of fish present in a given area is obviously of great importance to their behavioural interactions. This experiment was designed to discover the effect of density of brown trout upon their aggressive behaviour in two different environments. It was expected that density would affect aggression in both 'Natural' and 'Artificial' environments, but that this effect would be modified to some extent by the environment type.

1.4.2.

Materials and Methods The equipment used in this experiment is described in Section 3 of the Appendix. In addition, each aquaria contained a thermometer which was taped to the front glass panel to allow the temperature to be recorded without disturbing the fish.

Those aquaria representing natural environments were provided with a 5 - 15mm of coarse gravel, various sized stones and two clumps of moss. Every attempt was made to ensure that each Natural environment was the same with regard to spacing of stones and moss but use of natural materials made this, strictly speaking, impossible. Artificial environments were represented by bare aquaria with clean glass walls.

The fish used were juvenile brown trout, aged between 12 and 13 months and 7-10cm in length. Each of the three experimental runs used sixty fish which were taken at random from an outdoor stock tank. (See Section 6 of the Appendix.) The fish were placed in groups of 2, 4, 6, 8 or 10 fish per aquarium and whilst the two lower-density groups were size-matched there was some variation in size in the larger groups.

Each experimental run followed the same pattern and took two weeks to
complete. The fish were introduced to the aquaria and were allowed a 'settling-in' period of seven days. During this time the fish became used to the aquarium and the feeding technique. In order to feed the fish with as little disturbance as possible each aquarium had a feeding tube of flexible P.V.C. Before the start of the observation period a small amount of food was blown through the tube on to the surface of the water. The fish usually accepted this method of feeding within three or four days of introduction to the aquarium and fed confidently thereafter. Commercially prepared pelleted trout food was used and although there was no strict rationing the amount of food was in proportion to the number of fish.

After the settling-in period were five days of observation. Each aquarium was observed for 15 minutes in the morning and afternoon. As feeding is known to affect the aggressive behaviour in trout (e.g. Hartman, 1963) each group of fish was fed exactly ten minutes before observation began. Records of the aggressive behaviour were kept on a grid chart which was divided into three sections of five minutes duration and separate tallies were kept of five categories of aggression viz: threats by a dominant fish; threats by a subordinate fish; nip/chase by a dominant fish; nip/chase by a subordinate fish; retaliations. In the second and third experimental runs frontal and lateral threats were recorded separately.

Temperatures were recorded twice daily in the settling-in period and at the beginning of each observation period.

At the end of an experimental run the fish were removed to a separate stock tank, the aquaria were cleaned and restocked for the next run.

1.4.3

Results The results of this series of experiments are shown in Fig. 1.1 a and b. The difference in 'total aggression' between the
Fig 1:1 Aggressive behavior of juvenile brown trout at different fish densities and in two environment types. Aggression expressed as:

- total number of aggressive acts recorded in 2.5 hours,
- aggressive acts per fish per hour.

- Artificial environments
- Natural environments
the two environment types is immediately obvious. There are also different relationships between aggression and density in the two environment types. When the data are expressed as aggressive acts per fish per hour (fig. 1.1b) a peak is seen in the Artificial environments, compared with an almost linear Natural environment relationship.

Presentation of the data in the form of aggressive acts per fish per hour may lead to confusion because no account is taken of the changing social structure of the groups of fish. As there was only one dominant fish present in each group studied, an increase in total density represented an increase only in the density of subordinate fish. When the data are converted to show the reaction of dominants and subordinates to increased subordinate densities, fig. 1.2, it can be seen that the aggression of dominant fish increased with increasing density in both environments. In the Artificial environment dominant aggression increased rapidly up to the six-fish density, beyond which the rate of increase slowed, levelling off at the two higher densities. Dominant aggression in the Natural environment increased at a much slower rate but showed no sign of levelling off at the densities tested.

The density/aggression relationship for subordinate fish was very different. Although subordinate aggression did increase with density in both environments the rate of increase was extremely low. There was no significant difference (P = 5.0%) in the levels of subordinate aggression between the two environments.

When the data were broken down into the components of aggressive behaviour it was found that some were affected by density and/or environment type and others were largely independent of one or both of these variables.
Fig 1-2 Aggressive behaviour of dominant and subordinate juvenile brown trout at different fish densities and in two environment types.
AE Artificial environment
NE Natural environment
S Subordinate
D Dominant
If the percentage of the total aggression performed by dominant fish is examined (Table 1.4) it is seen that environment type had no great effect. From 100% aggression by the dominant at the two fish density in both environments, the percentage decreased sharply with increasing density, levelling off at densities of eight and ten fish.

In Fig. 1.3 the number of threats and the number of nip/chases in both types of environment for dominant and subordinate fish is shown and it can be seen that the dominant fish's aggression consisted largely of nip/chases with low threat levels while the subordinate fish had similar levels for both components. Density affected nip/chases and threats in the same sort of way as it affected total aggression and the environment type difference can be recognised in these components.

The frequency of threats relative to that of nip/chases (the nip/threat ratio) was affected by density for both dominant and subordinate fish. However, from Fig. 1.4 it can be seen that while dominant fish were only slightly affected the nip/threat ratio of subordinates underwent considerable change with increasing density. At low densities subordinates threatened considerably more than they nipped. As density increased the relative number of nips increased until at the highest densities subordinates nipped as often as or slightly more than they threatened. Dominant fish consistently nipped much more than they threatened. In Natural environments the dominant fish nipped relatively more with increasing density. In the Artificial environments dominant fish nipped relatively more up to a density of four fish, whereas thereafter there was a decline at higher densities to levels similar to those in Natural environments.

The numbers of threats recorded were made up of frontal and lateral threats. By far the greater part was frontal threats, independent of
TABLE 1.4

Aggressive Behaviour of Dominant Fish as a Percentage
of the Total Recorded Aggression at Different Fish
Densities and in Two Different Environment Types

<table>
<thead>
<tr>
<th>Number of Fish per Tank</th>
<th>Environment Type</th>
<th>Percentage Aggression by Dominant</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>Natural</td>
<td>100.0</td>
</tr>
<tr>
<td>4</td>
<td>&quot;</td>
<td>99.5</td>
</tr>
<tr>
<td>6</td>
<td>&quot;</td>
<td>77.2</td>
</tr>
<tr>
<td>8</td>
<td>&quot;</td>
<td>72.6</td>
</tr>
<tr>
<td>10</td>
<td>&quot;</td>
<td>64.9</td>
</tr>
<tr>
<td>2</td>
<td>Artificial</td>
<td>100.0</td>
</tr>
<tr>
<td>4</td>
<td>&quot;</td>
<td>91.4</td>
</tr>
<tr>
<td>6</td>
<td>&quot;</td>
<td>61.0</td>
</tr>
<tr>
<td>8</td>
<td>&quot;</td>
<td>70.8</td>
</tr>
<tr>
<td>10</td>
<td>&quot;</td>
<td>65.7</td>
</tr>
</tbody>
</table>
Fig 13. Components of aggressive behaviour of dominant and subordinate juvenile brown trout at different fish densities and in two environment types. 
D Dominant; S Subordinate; N Nip; T Threat
Fig 1-4 Relative frequency of threats and nips by dominant and subordinate juvenile brown trout at different fish densities and in two environment types.
AE Artificial environment
NE Natural environment
S Subordinate
D Dominant
density and environment type and although the percentage frontal threats for dominants and subordinates was slightly higher for Natural environments there was no real difference, the percentage frontal threats being between 85 and 100% in all cases (Table 1.5).

The only two mortalities in the experiment were both in the same aquarium, which had a Natural environment and a density of two fish. In the first instance, the subordinate fish disappeared after the sixth observation, presumably by leaping out of the aquarium (although the aquaria were covered there were small gaps at each end for the siphons). In the second instance the subordinate fish was attacked repeatedly and died after six observations. Most of the scales from both shoulders had been knocked off and the head was cut in several places. Also, this fish was never seen to eat.

The grouping of subordinate fish as seen in BE1 was again noticeable at densities of over four fish per tank in the Artificial environments, when most of the subordinates huddled together, invariably near the surface of the water and in one corner of the aquarium. The dominant in this situation usually rested on the bottom or 'patrolled' the aquarium, frequently attacking subordinates. The Natural environment subordinates usually lay on the bottom, separate from one another and the dominant kept position at about midwater, often near a stone or clump of moss. Because of the relatively slow flow rate (not enough to cause positive rheotaxis) no true territorial behaviour was seen but some fish, especially dominants in the Natural environments, showed marked preferences for a certain position or lie. Such positioning was less noticeable in Artificial environments.

As in BE1, movement of subordinates was important to the dominants' aggression especially in Natural environments. Whilst Artificial environment dominants would frequently swim towards and attack one
<table>
<thead>
<tr>
<th>Number Fish Per Tank</th>
<th>Environment Type</th>
<th>Total Dominant Threats</th>
<th>Total Subordinate Threats</th>
<th>% Frontal Threats by Dominant</th>
<th>% Frontal Threats by Subordinate</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>Natural</td>
<td>1</td>
<td>0</td>
<td>100.0</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>&quot;</td>
<td>8</td>
<td>18</td>
<td>100.0</td>
<td>94.4</td>
</tr>
<tr>
<td>6</td>
<td>&quot;</td>
<td>33</td>
<td>36</td>
<td>67.8</td>
<td>94.4</td>
</tr>
<tr>
<td>8</td>
<td>&quot;</td>
<td>54</td>
<td>32</td>
<td>87.5</td>
<td>87.0</td>
</tr>
<tr>
<td>10</td>
<td>&quot;</td>
<td>46</td>
<td>60</td>
<td>90.0</td>
<td>100.0</td>
</tr>
<tr>
<td>2</td>
<td>Artificial</td>
<td>22</td>
<td>0</td>
<td>100.0</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>&quot;</td>
<td>119</td>
<td>59</td>
<td>84.8</td>
<td>86.4</td>
</tr>
<tr>
<td>6</td>
<td>&quot;</td>
<td>161</td>
<td>170</td>
<td>89.4</td>
<td>86.4</td>
</tr>
<tr>
<td>8</td>
<td>&quot;</td>
<td>135</td>
<td>231</td>
<td>83.7</td>
<td>87.0</td>
</tr>
<tr>
<td>10</td>
<td>&quot;</td>
<td>89</td>
<td>263</td>
<td>85.3</td>
<td>90.87</td>
</tr>
</tbody>
</table>
particular fish, Natural environment dominants tended to attack only those subordinates which swam close to them. If a subordinate approached an Artificial environment dominant it was always attacked, usually more 'fiercely' than was normal.

1.4.4 Discussion

The way in which environment type modified the effect of density upon aggressive behaviour was largely as expected but detailed analysis of the data revealed a complicated situation. The effect of density and/or environment type was found to differ between dominant and subordinate fish. Also the composition of aggressive behaviour was influenced by density and environment type.

With increasing density there was a much greater increase in total recorded aggression in the Artificial environment. It is likely that this difference was caused by higher densities being more apparent to the fish in the Artificial environments with more visual contact between fish than in the Natural environments. The greater activity of the fish in Artificial environments may have been another contributory factor.

The decline in the number of aggressive acts per fish per hour in the Artificial environments at densities of over six fish per tank (Fig. 1.1b) occurred because the dominant fish in each group was responsible for most of the aggressive behaviour. Each dominant fish had a finite capacity for aggression. With increased numbers of subordinates, a dominant would be able to exhibit increased rates of aggression only up to its own maximum. At higher densities, the rate of dominant aggression would remain approximately constant but the rate of aggression per fish for the whole group would decline, as was observed. These results are similar to those of Keenleyside and Yamamoto (1962).
In the present experiment the maximum rate of dominant aggression was 200-220 acts per hour in the Artificial environment (Fig. 1.2). Maximum aggressive performance of Natural environment dominants was much lower, at 70 acts per hour. Presumably, if higher densities had been used, aggression by Natural environment dominants would have reached maximum rates similar to that observed in Artificial environments.

The very similar reactions of subordinates' aggressive behaviour to increased density in both environments suggests that the dominant fish inhibited subordinate aggression to a large extent. The inhibition of subordinate aggression was strong enough to prevent any great rise of aggression with increasing density, although there was slight positive correlation in both environment types. The observed changes in composition of subordinate aggressive behaviour, with the fish threatening more than nipping at low densities and vice versa at high densities, may have been brought about by threat postures becoming less effective at higher densities.
As the final experiment of this part of the investigation, BE3 was designed to examine how environmental complexity brought about reduction of aggression. To do this, the effects of different types of structure upon the aggressive behaviour of groups of fish were tested and compared with control groups of fish maintained in simple environments. It was expected that results would provide some indication as to which factors were important in limiting aggressive behaviour.

BE3 was made up of three individual experiments. First, a preliminary experiment was carried out in the tanks from BE1 to establish whether or not an environment changing in complexity with time caused corresponding changes in aggressive behaviour. The results suggested that further work was worthwhile but that different equipment, namely much larger tanks, would be needed.

After the design and construction of the new tanks, another preliminary experiment was performed, similar to the original small-tank experiment, to confirm that the aggression/complexity effect was real and not an artefact of the small tanks.

The final experiment of BE3 was also carried out in the new tanks but with slight modification to the method used and replication of runs.

Small-Tank Preliminary Experiment, Materials and Methods

This experiment was performed in the same tanks as used in BE1. (Section 2 of the Appendix).

The structures used to provide complexity were designed to contain some of the components of the 'Natural environments' of BE1 and BE2. Each
structure was made on a 15 x 15cm base of rigid 3mm P.V.C. A typical structure is shown in Fig. 1.5. The plastic egg-containers were chosen because they provided a readily available, easily repeated, but complicated shape. The arrangement of the three types of object upon the base was the same on each of the 12 structures made.

A group of six fish was used in each tank. Nominal length of the fish was 10.0cm but actual size ranged from 8.4 to 11.9cm.

Only one run was performed in these tanks. A second run was attempted but four of the control fish died on day 2 and three of the experimental fish on day 3, so the run was abandoned. Experimental procedure was as follows. The groups of fish were introduced to the tanks in the morning of day 1. Neither tank contained any structures. For the remainder of day 1, and for as long as was possible on days 2 and 3, the fish were observed and notes were made to enable individual recognition of each fish. Recognition was on the basis of pigmentation, size and fin condition. Individual fish were allocated numbers, as in BE1.

The fish were fed by means of the 'remote-control feeder' described in Section 7 of the Appendix. Feeding was carried out once on day 1 and twice daily thereafter, the fish quickly becoming accustomed to the source of food.

Recording of aggressive behaviour was begun on day 4, each observation period following the same pattern. The group of fish was observed for 25 minutes and each aggressive act was recorded on a grid chart and classified as to which fish initiated the act and which fish was the subject of the act. At the end of 25 minutes, the fish were fed for 10 minutes, during which time food pellets were introduced at the same rate as they were eaten, avoiding accumulation of uneaten pellets. Immediately after feeding the aggressive behaviour of the fish was
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A group of six fish was used in each tank. Nominal length of the fish was 10.0cm but actual size ranged from 8.4 to 11.9cm.

Only one run was performed in these tanks. A second run was attempted but four of the control fish died on day 2 and three of the experimental fish on day 3, so the run was abandoned. Experimental procedure was as follows. The groups of fish were introduced to the tanks in the morning of day 1. Neither tank contained any structures. For the remainder of day 1, and for as long as was possible on days 2 and 3, the fish were observed and notes were made to enable individual recognition of each fish. Recognition was on the basis of pigmentation, size and fin condition. Individual fish were allocated numbers, as in BE1.

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Fig 1-5 Design of structures used to provide environmental complexity in BE3.

B Base plate
C Segment of white plastic beaker
E Section from plastic egg-package
H Line of 1mm holes
U Upstream edge of structure
W Green nylon wool strands, 10cm long

scale 1:1.5
recorded for a further 25 minutes. Each complete observation period
thus took one hour.

Each group of fish was observed once in the morning and once in the
afternoon of each test day of the experiment. The two tanks were
always observed in the same order, the time between feeding of each
group was thus kept the same.

After the two day 'settling-in' period the experiment was composed of
four stages, each stage lasting two days and including four observation
periods. In stage 1, (days 3 and 4) the two tanks were the same, with
no structures present in either. After the second observation period of
day 4 two of the structures were placed in Tank B, chosen as the
experimental tank by the toss of a coin, with Tank A left bare as a
control. No observations were made on day 5 as the fish were allowed
one day to become used to the presence of the structures. Day 6 was the
start of stage 2 which lasted until day 7. Similarly, stage 3, with a
total of four structures added to the experimental tank, occupied days
9 and 10 and stage 4, with a total of six structures in the experimental
tank, took place on days 12 and 13.

The positions of the structures in the experimental tank are shown in
Fig. 1.5.

1.5.3

Results In this experiment a complete set of observations was
possible only for the experimental group of fish. In the control group
observations were obtained for the first two stages but between stages
2 and 3 one of the fish died. If this fish had been replaced it would
have altered the social composition of the group, consequently affecting
the aggressive behaviour of the other fish, rendering the group
unreliable as a control. Therefore the control group was discarded.
Fig 1-6 Distribution of structures in the experimental tank in stages 2, 3 & 4 of BE3 small-tank preliminary experiment.

S Structure
U Upstream end of tank

Scale 1:10
The cause of the control fish's death was a secondary fungal infection in wounds received during aggressive interactions with the dominant fish.

The number of aggressive acts recorded in each observation period is shown in Fig. 1. With increasing complexity (number of structures) the level of aggression fell in the experimental group of fish. In the control group the level of aggression in stage 2 appeared to be higher than in stage 1. The lack of replication and small sample number did not permit statistical analysis of this data.

In stage 2, while the control group was still complete, the behaviour of the two groups of fish was noticeably different. Although there were only two structures in the experimental tank there was usually one subordinate fish in each. Other subordinates in the experimental tank most often lay close to the floor of the tank unless chased by the dominant fish. During feeding the dominant appeared to eat proportionately more food than the subordinates but all of the subordinates fed.

In contrast, the subordinates in the control group were apparently inhibited during feeding and although they swam about in an agitated manner only one or two of the five actually fed. Before and after feeding the subordinates took up positions in the corners of the tank, usually near the surface and frequently formed tight bunches, or 'fright huddles' (Stuart, 1953, also BE1 and BE2).

1.5.4
Discussion
With the demise of the control group of fish half way through the experimental period, the results of this experiment cannot be regarded as reliable. Although the downward trend of aggression with increasing complexity of the environment may be taken to suggest
Fig 1.7 Aggressive behaviour of juvenile brown trout with changing environmental complexity.

- Experimental tank
- Control tank (No structures in any stage)

Experimental tank:
- Stage 1, no structures; Stage 2, 2 added; Stage 3, 4 added; Stage 4, 6 added.
that the structures used brought about reduced aggression, no reliability can be placed on this interpretation without a control.

Clearly, the design of the experiment was at fault. This was emphasised in the second run of the experiment when both control and experimental fish died in the first few days.

The most likely cause of mortality in the second run was that the fish wore too big for the tanks used. This created problems with keeping the small volume of water sufficiently purified and oxygenated. Another difficulty arising from the 'large fish/small tank interaction' was the reduced life of the subordinate fish.

In the control situation, the life expectancy of a subordinate fish may be regarded as inversely proportional to the amount of harassment it receives from the dominant fish. In a small tank, the dominant is almost continually aggressive, often causing physical damage to the subordinates and usually inhibiting their feeding. The subordinates are very quickly brought into extremely poor condition and are open to secondary fungal and bacterial infections which often cause death.

The solution to the problems caused by the size of the fish relative to the size of the tanks was to use either smaller fish or larger tanks. The latter course was chosen as, although smaller fish were available at certain times of the year, a long-term experiment would face difficulties from the small fish growing as it would be impossible to determine the exact size of fish at which the volume of the tank began to influence results.
1.5.5

Large-Tank Preliminary Experiment, Materials and Methods

The tanks designed and built for this experiment are described in Section 5 of the Appendix.

The structures used in this experiment were the same as those used in the small-tank preliminary experiment.

The fish used in this experiment were between 7 and 11cm in length. The same feeding method was used as in the previous experiment.

Two groups of 15 fish were taken from the outside holding tanks and introduced to the experimental tanks.

The fish were allowed two complete days to 'settle in' and to become accustomed to the light regime and the method of feeding. During these two days the fish were fed at approximately the same times as they would be fed in the experiment, 0945 and 1545h for Tank A and 1015 and 1615h for Tank B.

A single observation period took approximately 35 minutes to perform and was split into two sections. For the first 15 minutes the fish were observed and the number of aggressive acts recorded with a tally counter. Sub-totals were noted at three minute intervals. Because of the number of fish in the groups no attempt was made at individual recognition of the fish. At the end of the first 15 minutes the fish were fed for 90 seconds, timed from when the second food pellet was eaten. During feeding the pellets were introduced at a rate such that as few as possible remained uneaten. After the 90 seconds of food introduction the fish were allowed a further 90 seconds to eat any food pellets that did remain. Immediately after the three minutes of feeding there was a second 15 minute period of aggression monitoring, with 3-minute sub-totals.
This method of observation allowed comparison of levels of aggression before and after feeding, as well as eliminating any possible difference in aggression between the two tanks caused by different times between feeding and observation.

The experiment was made up of four stages, each following the same sequence. Both groups of fish were observed in the morning and afternoon for the first two days of a stage, and in the morning only of the third day, a total of five observations per group per stage. Immediately after the third day's observation, both tanks were cleaned by siphoning and the necessary changes were made to the experimental tank. To allow the fish to recover from the disturbance caused by the cleaning and alterations to the experimental tank, no observations were made in the afternoon of the third day, neither were the fish fed. The time between the last observation period of one stage and the first of the next was 24 hours.

For the first stage of the experiment neither tank contained any structures and both were in the control condition. At the end of stage 1 the experimental tank was determined as Tank A by the toss of a coin and six of the structures were added. Tank B was left in the control condition. In stage 3 there were 12 structures in Tank A with Tank B still as a control but for stage 4 the 12 structures were removed from Tank A and introduced to Tank B. The distribution of the structures in stages 2, 3 and 4 is shown in Fig. 1.8

1.5.6

Results

Fig. 1.9 shows the effects of changing environmental complexity upon the number of aggressive acts recorded for the groups of fish. When the results were analysed by a Two-Factor Anovar, it was found that there was no significant difference in aggression between the two tanks in stage 1. In stages 2, 3 and 4, there were significant
Fig 1.8 Distribution of structures in stages 2 & 3 of BE3 large-tank preliminary experiment.

S Structure
U Upstream end of tank
Fig 1-8 Distribution of structures in stages 2 & 3 of BE3 large-tank preliminary experiment.

S  Structure
U  Upstream end of tank
Aggressive behaviour of juvenile brown trout with changing environmental complexity.

Stage 1: Tanks A & B in control condition
Stage 2: Tank B as control, 6 structures in A
Stage 3: Tank B as control, 12 structures in A
Stage 4: Tank A as control, 12 structures in B
15 Fish per tank
differences in levels of aggression between tanks with $P = 0.1\%$, $1.0\%$ and $0.1\%$ respectively. There was an effect of time upon aggression significant at $P = 1.0\%$ in stage 1 and at $P = 5.0\%$ in stage 2 but no significant effect of time was found in stage 3 or 4.

In tank A, there were significantly ($P = 5.0\%$) fewer aggressive acts in stage 2, with six structures, than in stage 1, with none. There was no significant difference between numbers of aggressive acts in stage 2, with six structures, and stage 3, with twelve structures.

In tank B there were significantly ($P = 5\%$) more aggressive acts in stage 2 than stage 1, and significantly ($P = 5\%$) more aggressive acts in stage 3 than stage 2.

The changeover of levels of aggression in stage 4 strongly suggests the presence of the structures was responsible for the lower levels of aggression observed in the experimental tanks.

The dominant fish in each group was easily identified by its paler colouring and lack of contrasting parr-marks or spots. The behaviour of the dominants was similar in both experimental and control groups. Typically, the dominant would divide its time between resting, at about mid-water or slightly lower, and being aggressive towards subordinate fish. The amount of time occupied by aggression was relatively greater in the observation period following feeding than that before and overall the dominant was responsible for most of the aggression.

Subordinate fish's behaviour was affected by whether or not there were any structures present in the tank. In the control condition the subordinate fish were usually in a loose shoal in the upstream half of the tank, most often in the upper half of the water. When structures were available at least two and occasionally as many as five, were occupied at any particular time. The structures most often occupied
by the fish were those nearest to the location of the shoal of subordinates. When a remote structure was occupied, it was normal for the fish to remain in the structure for relatively long periods and not leave it to feed. Subordinates not using the structures tended to form shoals, as in the control condition.

Usually the dominant fish fed first and ate most but the severe inhibition of feeding by subordinates seen in the small-tank preliminary experiment was not apparent in the large tanks.

One aspect of feeding which was especially noticeable in both experimental and control groups of fish was the almost complete cessation of aggression during the introduction of food. Although feeding brought about a rapid increase in activity, which persisted into the post-feeding observation period and may well have been associated with the higher levels of aggression recorded after feeding, it was extremely rare to see aggression of any sort during feeding. Any social distinction between dominants and subordinates that was discernible before feeding disappeared with the introduction of food.

No evidence of any territoriality was seen in either the control or experimental group of fish. The most probable reason for this is the slow flow of water through the tanks (Kalleberg, 1958).

1.5.7

Discussion The results of this experiment demonstrated that the addition of 'complexity' (structures) to the environment of a group of juvenile brown trout had the effect of causing significantly reduced levels of aggressive behaviour.

The reduction in aggression, though, was not proportional to the amount of 'complexity' (number of structures) as can be seen from fig. 1.3, stages 2 and 3, Tank A. It is not obvious why this should have been
so but there are several possible reasons. The low rate of flow through the tanks prevented the formation of territories by dominants or subordinates. Instead, the fish formed a loose shoal about 10-15cm above the bottom. In this situation the number of structures occupied by fish may have been limited, not by the number of structures available, but by the reluctance of the fish to maintain a stationary position on the bottom of the tank.

Another factor which may have contributed to the failure of an increase in complexity to bring about a further reduction in aggression was the small size of the structures (4.5cm high) relative to the depth of the water (31.5cm). As the fish maintained a position approximately in mid-water, the increase in the number of structures from stage 2 to 3 may not have been as apparent to the fish as it would have been if they maintained position on the floor of the tank.

The structures used in the experiment contained several components of a 'natural environment' but those most likely to have been involved in the reduction of aggression were the visual segregation caused by the structures and the availability of overhead cover to the fish. Of the two, the latter would seem to be the more important in this case as the combination of the positioning of the fish and the size of the structures provided little visual segregation.

In order to determine the way in which these two components, visual segregation and availability of overhead cover, acted to reduce aggression, the third experiment in the series was designed to compare the effects of different types of structure upon aggressive behaviour in groups of fish.

1.5.8

**Large-tank Second Experiment, Materials and Methods**

The same apparatus was used as in the preliminary experiment (Appendix, Section 4) but modifications were made to the experimental procedure. First, as the
number of structures used in the preliminary experiment had little
effect upon the degree of reduction in aggression, it was decided to
use only three stages in this experiment; stage 1 with both tanks in
the control condition, stage 2 with one tank as a control, the other
with structures, and stage 3 with conditions reversed between the tanks.

The group of fish in the tank which received structures in stage 2 was
described as the S-2 group and the group receiving structures in stage 3
was the S-3 group.

The settling-in period was reduced to 24 hours.

The second modification was to the design of the structures used, each
new type of structure incorporating only one of the components thought
to reduce aggression.

Four different structures were devised, and are described below;

a) **Tunnels** These structures were made from 9mm rigid P.V.C. of the
same colour as the tanks. These structures were simple, low covers.
The rectangular roofs of the tunnels measured 10 x 12.5cm, with long
sides 3.5cm in height. The short sides were left open, allowing fish
to enter the structures.

b) **Blocks** The blocks were made of the same material as the tunnels
and were of the same dimensions, the only difference being that the
short sides were blocked off, preventing fish from entering.

c) **Planks** Planks were constructed from 3mm sheets of rigid P.V.C.
and were 19cm long and 15cm high. They were supported by two struts
of the same material, measuring 1.5 x 13cm, jointed into the sheets.

d) **Banks** As these structures needed to float they were made from
5mm marine plywood, rectangular in shape with sides of 15 and 57 cm.
The banks were secured in the desired position by lengths of 0.5mm
diameter stainless steel wire attached to the banks and to the Dexion tank-frame.

Six of the type a), b) and c) structures were made and two of type d).

The four types of structures can be regarded as two pairs. The tunnels and blocks were both the same size, the only difference being that fish could not enter the blocks. The planks and banks, although different in number, had the same total surface area (1710cm²). Whilst the planks provided minimum overhead cover and maximum visual segregation, the banks provided maximum overhead cover but no visual segregation.

Comparisons may also be made between the tunnels and banks as both types of structure provided overhead cover, but of different natures, and between blocks and planks as these two structures had approximately the same total surface area.

Figure 1.10 shows the design of the structure types and their distribution in the experimental tanks.

The observation periods were carried out in the same way as in the large-tank preliminary experiment, with 15 minutes pre-feeding observation, 90 seconds feeding and 15 minutes post-feeding observation. With each experimental run reduced to three stages, the time taken for each run was ten days.

A total of eight runs was performed, with two replicates for each structure type. In the first run for any particular structure, the tank to receive the structures in stage 2 was chosen by tossing a coin. In the second run the order was reversed. For example, in run 3, the first run using planks, the S-2 group was in Tank B and in run 7, the second planks run, Tank A contained the S-2 group.

In addition to records of aggressive behaviour, notes were made on the general behaviour and distribution of the fish and their reaction to
Fig 1.10 Design and distribution of structures used in BE3, large-tank second experiment.

- **S**: Position of Tunnels, blocks & planks.
- **B**: Position of banks.
- **U**: Upstream end of tank.
the various structure types.

Information on the wigwag display, recorded during this experiment is presented separately.

1.5.9

Results a) Tunnels The results of the two runs using tunnels are shown in Fig. 1.11. A Two-Factor Anovar indicated that for stage 1 there was no significant difference in the numbers of aggressive acts recorded in the two tanks. There was an effect of time significant at $P = 0.1\%$. In stage 2, the effect of time was not significant but there was a difference, significant at $P = 1.0\%$, between the levels of aggression in the control and experimental conditions. In stage 3 there was again no significant effect of time but the effect of condition was significant at $P = 0.1\%$. From Fig. 1.11 it is seen that in stage 2 the S-3 groups had the higher level of aggression and that in stage 3 this was reversed with the S-2 groups having the higher aggression level.

The reaction of all the groups of fish to the presence of the tunnels was similar. Once the tunnels had been added to the tank it was rare to see all 15 fish at the same time. Usually, there was at least one tunnel occupied by a fish and on occasion four of the tunnels were occupied. In normal circumstances only one fish occupied any one tunnel. During any particular observation period it was noticeable that the same fish used the tunnels, although when one of these fish left a tunnel, to feed for instance, it did not always return to the same one.

The length of time that fish stayed in the tunnels varied greatly, from a few seconds up to 25 minutes but usually a fish would remain stationary inside the tunnel until it was stimulated to leave, either by the sight of food and feeding fish or by being involved in an aggressive interaction.
Fig 1:11  Aggressive behaviour of juvenile brown trout with changing environmental complexity
Stage 1  Both groups in control condition
Stage 2  S-3 group as control  S-2 group with 6 tunnels
Stage 3  S-2 as control  S-3 with 6 tunnels
Dominant fish made very little use of the cover afforded by the tunnels. Occasionally a dominant would swim through a tunnel but would not remain 'inside' for any length of time.

Of the subordinate fish it was the larger individuals which made most use of the tunnels. Subordinates not using the tunnels formed loose shoals, above the level of the tunnels and frequently situated in the upstream half of the tank.

The tunnels were involved in the aggressive behaviour of the groups of fish in several ways, the most frequent of which was when a fish swam into a tunnel already occupied. Whenever this was observed the result was always a violent aggressive interaction resulting in one of the fish being 'evicted' from the tunnel. Whether the occupant or the intruder gained final possession of the tunnel appeared to depend on the direction from which the intruder approached.

The occupant of a tunnel always lay with its snout just outside the opening. If an intruding fish entered the tunnel from behind the occupant it was practically always the intruder that gained final possession. If, however, the intruder approached the tunnel facing the occupant the outcome was reversed with the original occupant retaining possession.

Another way in which the tunnels were involved in the aggressive behaviour of the fish was observed less frequently and consisted of the occupant of a tunnel swimming out and attacking other fish, whether or not they were attempting to enter the tunnel. This sort of behaviour could perhaps be interpreted as a defence of the tunnel by the occupant but this is unlikely as the occupants rarely returned to the original tunnel but remained 'outside' or, occasionally, entered a different tunnel.
Behaviour which could be recognised as territorial defence was seen on only two occasions. In these instances the fish used one of the tunnels as the focal point of its territory and emerged only to feed or to attack other fish which were close to the opening of the tunnel. After such excursions the territory-holding fish returned to the original tunnel.

Although the tunnels were involved in aggressive interactions of the fish in the situations described above, it was most noticeable that the tunnels were not used as escape routes or refuges by fish being attacked. Subordinates pursued by the dominant or by a larger subordinate were never seen to enter the tunnels but tried to evade a pursuing fish by swimming faster, rapidly changing direction or by exhibiting a submissive posture.

In all groups of fish observed, the tunnels were used extensively as fright cover when the fish were subjected to overhead disturbance. This occurred at the end of stage 2, when the tunnels were transferred to the S-3 tank and at the end of the run when the fish were removed. If a net or an arm was moved suddenly over the tank the immediate reaction of the fish in the experimental condition was to enter the nearest tunnel. In such a situation as many as five fish were to be found under the same structure and if the tunnel was gently moved along the bottom of the tank the fish often moved within it and maintained their hidden position.

When the fish were frightened there was a complete cessation of aggression and this may have allowed more than one fish to stay in the tunnels, in contrast to the undisturbed condition where only one fish per tunnel was the norm.

Fish in control conditions reacted differently to overhead disturbance and showed very rapid, panicky swimming in all directions in the first few seconds, followed by aggregation in 'fright huddles' (Stuart, 1953,
Brown et al. (1970) and Mason & Chapman (1965), in the corners of the tank furthest from the source of the disturbance. As in the experimental condition there was a cessation of all aggressive behaviour in the frightened groups of fish.

b) Blocks  Figure 1.12 shows the results obtained in the runs with blocks as the structures. Statistical analysis of the data indicated that in stage 1 there was no significant difference in aggression between tanks. Nor was there a significant effect of time. In stage 2, time had no significant effect but there was a significant effect of conditions upon aggression, at $P = 5.0\%$ with the S-3 tank having the higher level of aggression. There was no significant effect of time upon aggression in stage 3 and condition had no significant effect although the S-3 group of fish showed a slightly higher level of aggression.

The groups of fish were consistent in their reaction to the presence of the blocks in that these structures made no apparent difference to the behaviour or distribution of the fish.

There was no indication of any attachment of the fish to the blocks, nor was any aggressive behaviour associated with them. With blocks in the tanks, the location of the fish was virtually the same as that seen in the groups of fish in the control condition, the only difference being that the shoals of fish were slightly higher in the water over the blocks, usually 10-15cm below the surface.

No evidence of any territorial behaviour was seen in tanks containing blocks.

When groups of fish in the experimental condition were subjected to overhead disturbance their reaction was the same as that of fish in control conditions, with panic-swimming and 'fright huddles'. The
Fig 1.12  Aggressive behaviour of juvenile brown trout with changing environmental complexity
Stage 1  Both groups in control condition
Stage 2  S-3 group as control  S-2 group with 6 blocks
Stage 3  S-2 as control  S-3 with 6 blocks
blocks were not used as fright cover.

c) Planks  Results from the two runs using planks as the structures are shown in Fig. 1.15. The effect of time upon aggression was significant at $P = 5.0\%$ in stage 1 but was not significant in stages 2 or 3. The results obtained with the planks differ from those for the other structures in that the S-3 and S-2 groups of fish had significantly ($P = 5.0\%$) different levels of aggression in stage 1, with the S-2 groups exhibiting more aggression.

In stage 2 there was a difference significant at $P = 0.1\%$ between conditions, with the S-2 groups of fish now showing the lower level of aggression. An effect of condition significant at $P = 0.1\%$ was found for stage 3, S-2 groups having the higher level of aggression.

The groups of fish were consistent in their reaction to the presence of the planks. There was very little association between the fish and the planks in an undisturbed state, although rare instances of subordinate fish lying in the angle of a plank and one of its supports were seen.

The main effect of the planks was upon the distribution of the fish throughout the depth of the water. Whilst fish in the experimental condition formed a typically loose shoal, it was noticeable that the shoal was located above the level of the tops of the planks. After feeding this distribution changed and between five and nine fish often remained below the level of the tops of the planks, presumably searching for food. This splitting up of the group after feeding may have been a contributory factor to the reduced aggression seen in tanks in the experimental condition.

The planks were involved directly in the aggressive interactions of the fish but not as any aspect of territorial behaviour. When two fish were showing aggressive behaviour, either displaying to one another or with
Fig 1.13 Aggressive behaviour of juvenile brown trout with changing environmental complexity.
Stage 1 Both groups in control condition
Stage 2 S-3 group as control S-2 group with 6 planks
Stage 3 S-2 as control S-3 with 6 planks
one fish chasing the other, it often happened that the two contestants
would pass either side of a plank, or that one of the fish would,
apparently unintentionally, move behind one of the structures and out
of sight of its opponent. Such visual segregation of the two contestants
was not inevitably the end of the interaction, though, as displaying
fish occasionally maintained their aggressive postures until they had
swum the length of the plank and were once again visible to each other.

Planks were not used as fright covers. Overhead disturbance of the groups
of fish in experimental conditions resulted in the typical 'fright
huddles' of fish in control conditions.

d) Banks. Figure 1.14 shows the results of the runs using banks to
create the experimental condition.

Analysis of the data by a Two-Factor Anover showed that in stage 1 there
was a significant effect of time upon aggression at $P = 0.1\%$; in stage 2
the effect of time was significant at $5.0\%$ but was not significant in
stage 3.

There was no significant effect of condition in stage 1 but the effect of
condition was significant, at $P = 0.1\%$, in stages 2 and 3. From Fig. 1.14
it can be seen that in stage 2 the S-3 groups of fish had the higher
levels of aggression, and in stage 3 the S-2 groups had the higher levels.

All groups of fish showed a similar reaction to the banks in that the
shoals of subordinate fish tended to avoid the areas of shade created by
the banks. The typical location of the shoal was approximately opposite
the upstream bank. Infrequent use of the cover provided by the banks
was made by individual subordinates but the amount of time spent under
the banks was short when compared with the time spent by fish under the
tunnel structures.

Only one instance of any attachment to one of the banks was seen and on
Fig 1.14  Aggressive behaviour of juvenile brown trout with changing environmental complexity  
Stage 1  Both groups in control condition  
Stage 2  S-3 group as control  S-2 group with 2 banks  
Stage 3  S-2 as control  S-3 with 2 banks
this occasion a subordinate fish maintained a position near the surface under the upstream bank for approximately 12 minutes. This particular subordinate was among the largest fish in the group and on four occasions was seen to chase other subordinates away from the bank and then return to its original position. The dominant fish ended this occupation of the bank by repeatedly attacking the subordinate until it no longer returned to the bank.

No other defence of a position was seen but other cases of temporary occupation of one of the banks by subordinate fish did occur. Usually, the 'period of residence' was short, the longest time observed being two minutes, and ended with the dominant chasing the subordinate out of the shaded area.

When groups of fish with banks were disturbed, the fish made use of the structures present as fright cover. As in all groups subject to disturbance, all aggressive behaviour ceased and all of the fish were under one or other of the banks. In undisturbed circumstances fish under the banks typically lay very near the surface of the water, usually close to the angle formed by the bank and the side of the tank but when disturbed the fish huddled together on the bottom of the tank, the group of fish being bounded by the area of shade produced by the bank.

a) Effect of Feeding upon Aggression The relationship between feeding and aggressive behaviour has been observed by many authors working with salmonids (e.g. Keenleyside and Yamamoto, 1962). A common observation is that aggression decreases or disappears during feeding but reappears at a higher level after feeding has stopped. This has been recorded for brown trout (Hartman, 1963), rainbow trout (Yamagishi, 1962 and Newman, 1956) and coho salmon (Chapman, 1962).

Symons (1968) suggested that deprivation of food leads to a strengthening of the social hierarchy in juvenile Atlantic salmon resulting from
dominant and subordinate fish responding differently to the lack of food, dominant fish becoming more and subordinates becoming less aggressive.

As well as feeding affecting aggression, there are instances of a reverse interaction, with aggression affecting feeding behaviour. For Smallmouth bass, Haines and Butler (1960) noticed that subordinate fish in stock tanks became emaciated and suggested that the cause was an inhibition of subordinate feeding by the aggressive behaviour of the dominant fish. Similar inhibition of subordinate feeding was seen in the small-tank preliminary experiment of this series.

In the present experiment feeding always had the immediate effect of reducing aggression to zero. This observation is in agreement with those of the authors referred to above but the levels of aggression after feeding were not always higher than the before-feeding levels. Instead there was a strong inverse relationship between time from the beginning of the experiment and the effect of feeding upon aggression, measured as \[ \frac{\text{No. of aggressive acts after feeding}}{\text{No. of aggressive acts before feeding}} \times 100\% \]

As there was no statistically significant difference in the effect of feeding on aggression between the S-2 and S-3 groups of fish, the two sets of data were combined and are presented in Fig. 1.15. An exponential curve was fitted to the data of Fig. 1.15, with \( r = -0.8726 \) (significant correlation at \( P = 0.1\% \)).

The data were tested to determine whether the length of the interval between successive feeds had any influence upon the effect of feeding on aggression but this parameter had no statistically significant effect.
Fig 1.15 Effect of feeding on aggression in BE3 Mean of all runs (See text for calculation)
Discussion  Addition of complexity, in the form of structures, to the environment of groups of juvenile brown trout affected aggressive behaviour within the groups of fish. However, the four types of structure used did not influence observed levels of aggression to the same extent.

Comparison of the effects of the different structure types is complicated by variation in the 'aggressive potential' (Jenkins 1969) of the groups of fish. Every group was composed of different individuals, each with its own capacity for aggression, some fish being relatively more aggressive than others. Consequently, some groups of fish possessed a higher proportion of 'aggressive' individuals than others and this was reflected in a large range of observed aggression among groups.

When testing the effect of a single type of structure, the differences in aggressive potential amongst the groups used was not important, as the switch-over of structures between stages 2 and 3 meant that all groups contributed to both control and experimental data for the structure in question. But, when comparing the effects of more than one type of structure, it is possible that differences in the aggressive potentials of groups of fish used could bias the comparison, as each group of fish contributed to the data of only one structure type.

To render the observed data for the four types of structure comparable, the following conversion was used.

In any experimental run, both groups of fish were in the control condition for two of the three stages and in the experimental condition for one stage. For the S-2 groups of fish, stages 1 and 3 were in the control condition and stage 2 in the experimental condition. For the S-3 group of fish, stages 1 and 2 were in the control condition.
From Figs. 1.11 - 1.14 it can be seen that, for any particular structure type, the levels of aggression in stages 2 and 3 for the groups of fish in the control condition were similar. Therefore, the base for the conversion of data for any given group was taken as the mean level of aggression for that group in its second stage in the control condition, and was termed the Mean Control Value (MCV). Results for the different structure types were then expressed as percentages of the relevant MCV.

In Fig. 1.16 the converted data for each of the four structure types is shown, with an 'overall control' (the mean of all individual controls) for stages 2 and 3. When these data were analysed by a Two-Factor Anovar the various structures were ranked in order of their effects upon aggression (Fig. 1.17).

The comparisons made possible by Figs. 1.16 and 1.17 confirmed that the four types of structure differed in their effect upon aggression, with tunnels and planks causing the lowest levels of aggression, banks showing an intermediate level and blocks having no significant effect when compared with the overall control.

If it is accepted that the different types of structure did differ in effect, possible reasons for these differences should be examined.

The four types of structures may be regarded as two discrete pairs, each pair allowing comparison of visual segregation and availability of cover as factors reducing aggression. When such within-pair comparisons are made, however, opposite conclusions are reached concerning the relative importance of the two factors.

For the tunnels/blocks pair, the visual segregation provided by the blocks had no significant effect upon aggression whilst the tunnels, by making cover available to the fish, brought about a reduction of aggression significant at $P = 0.1\%$. The conclusion reached from the
Fig 1.6 Data from BE3 converted to allow comparison of the effects upon aggression of the four structure types with a mean control. See text for calculation of MCV.
Fig 1.17 Diagramatic representation of the statistical analysis of data from stages 2 & 3 of BE3
Figures are % levels of significance
NSD No significant difference
Structure types ranked L to R in order of decreasing effect upon aggression
The results of this structure pair is that availability of cover is a more important factor in reducing aggression than visual segregation.

The results of the other structure pair, planks/banks, showed that both factors caused a significant reduction in aggression at \( P = 0.1\% \).

However, the significantly lower level of aggression (at \( P = 1.0\% \)) in the case of the planks suggested that visual segregation was a more important factor than the availability of cover in reducing aggression.

Whilst it appears, then, that both of the factors did act to reduce aggression, the effectiveness of the visual segregation structures was to a large extent influenced by other parameters and, although little direct data were obtained in this respect, the most likely source of this influence lay in the interaction between the distribution of the fish within the tanks and the size of the structures.

Distribution of the groups of fish was similar in experimental and control conditions. The typical situation of a loose shoal of fish located 10-20cm above the bottom of the tank was almost certainly the result of the velocity and depth of the water and was not affected to any great degree by any of the structures used. Similar distributions of trout in conditions of low water velocity have been observed by Kalleberg (1959) in a stream tank and by Keenleyside (1962) in natural conditions. Another factor which may have contributed to the distribution of the fish in this experiment was the bunching or huddling of subordinate fish. This has been observed in earlier experiments and has also been recorded for rainbow trout (Newman, 1956).

Because the fish were persistent in this distribution, visual segregation would only have occurred if the structures were large enough to coincide with the location of the fish. The planks, being 15cm high, were tall enough to intrude upon the location of the groups of fish and consequently interfered directly with the aggressive interactions of the
fish, especially after feeding, when some fish were nearer the bottom of the tank. This direct interference, coupled with a lower occurrence of fish-to-fish visual contacts resulted in a reduced level of observed aggression.

In contrast, the blocks, only 3.5cm high, did not coincide with the groups of fish and so did not directly interfere with aggressive interactions or reduce the number of fish-to-fish visual contacts. Consequently, the blocks had no effect upon aggression.

The depth of water in the tanks was also important in this respect. If the water had been shallower, it would probably have resulted in an increase in the visual segregation caused by the planks and may have brought about a situation where the blocks entered the location of the groups of fish. Had this happened, it would have been expected that the blocks would have led to a lower level of aggression than for the controls, but probably not as low as for the planks.

A consideration of the relative effects of the two structures providing overhead cover is perhaps more complicated than the case of the visual segregation structures because the main difference between the effects of the tunnels and banks was one of degree. Both structures caused a reduction in aggression significant at $P = 0.1\%$ when compared with the overall control but a comparison between the two structures showed a difference significant at $P = 1.0\%$ with the tunnels causing the lower aggressive level.

That the two structures providing overhead cover should have caused reduced levels of aggression at all is something of a puzzle. In the case of the tunnels it is possible that there was a reduction of apparent density when fish were occupying the tunnels but as the fish did not make extensive use of the structures it is difficult to understand why such a slight reduction in apparent density should have brought about the
observed reduction in aggression.

One factor which may have contributed to this disproportionate decrease in aggression was that it was the larger fish among the subordinates which made most use of the tunnels.

In any group of trout it is usually the largest individual which attains the dominant position (eg Newman 1956). During earlier experiments it was noticed that of the dominant fish's aggression a large proportion was directed towards the subordinates nearest in size to itself. Similar observations have been made on juvenile Atlantic salmon (Symons 1968). Presumably, this was because the largest subordinates presented more of a threat to the dominant's social position than did the smaller ones.

When tunnels were available and were occupied by the larger subordinates, this may have had the effect of making the prime target of the dominant's aggression temporarily inaccessible, thus causing a greater reduction in aggression than would have been expected on the grounds of apparent density alone.

It might also be suggested that the tunnels reduced aggression by eliciting territorial behaviour in the fish but this hypothesis does not merit serious consideration because of the low frequency with which territoriality was observed. To reduce aggression in this way the environment would firstly have to stimulate territorial behaviour in all individuals in the group and secondly the attachment of each fish to its own particular territory would have to be strong enough to maintain a territorial mosaic without frequent aggressive interactions. This was obviously not the case when the tunnels were used.

Similarly, it is most improbable that territorial behaviour was involved in the reduction of aggression when banks were the structures used. Also, because of the general tendency for the fish to avoid the banks in normal circumstances it seems unlikely that the banks caused any reduction
in apparent density, or made any of the subordinate inaccessible to the dominant.

Whilst the influence of apparent density reduction and temporary inaccessibility of subordinates may possibly account for the difference in the levels of observed aggression between the tunnels and the banks there still remains unsolved the question as to the cause of the reduced levels of aggression as compared with the controls when overhead cover was available.

The one aspect of the fish’s reaction which was common to both tunnels and banks was their use as fright cover. During the time spent watching the fish it was most noticeable that the cover afforded by the tunnels or banks was not used as a refuge from the aggressive behaviour of other fish in the groups. Only when the group of fish as a whole was subject to a common threat were the structures used as an escape or refuge. It was noticeable that in these situations the dominant fish did not have any advantage over the subordinates as one of the characteristics of the flight reaction was a suspension of all aggressive behaviour, which allowed several fish to share the same area of cover.

In the absence of any evidence of direct interference in aggressive behaviour by the tunnels or blocks the data would seem to suggest that these structures reduced aggression because they provided fright cover. There was, though, no apparent connection between the availability of fright cover and the level of aggression in groups of fish.

Stewart (1970) working with rainbow trout, demonstrated a strong inverse correlation between the light intensity beneath artificial structures and their use as fright cover. The light intensity beneath the tunnels was much less than beneath the banks because the former were much lower and had solid sides. If this is taken to mean that the tunnels would function better as fright cover than the banks, if availability of
fright cover influences aggression and if brown and rainbow trout react similarly in their preference for darker fright cover, then it might be expected that the tunnels would produce the lower levels of aggression, as was the observed case. This piece of tortuous argument might be regarded as support for the idea that the fish in this experiment reacted to the availability of fright cover by showing reduced aggression but is far from convincing.

Even if Stewart's data were admissible as support for the hypothesis that the reduced levels of aggression observed with tunnels and banks were associated with the degree of fright cover provided by these structures, they still offer no suggestion as to the nature of the association.

The main difficulty in solving the problem of why the availability of fright cover should lead to reduced levels of aggression arises from the fact that the process by which this reduction was achieved could not be directly observed or measured. Unlike the planks and blocks situation where aggression was seen to be reduced by direct interference in the mechanism of aggressive behaviour, the tunnels and banks must have acted largely in an indirect way.

It is feasible that the topography of the environment could reduce aggression by allowing it to fulfil its function and thus become temporarily redundant. In streams, aggression is the mechanism of territoriality. For a territory-holding fish faced with an intruding conspecific, the immediate function of aggression is to drive the intruder out of the territory and once this has been achieved aggression is no longer necessary and is no longer exhibited.

If a similar function-achievement could be identified in the present experimental situation it may follow that availability of cover reduced aggression in this way. The tanks used could be regarded as highly
stylised stream pools and thus aggression in the tanks may have the same function as in stream pools. Observations of trout in their natural environment have shown that in such pools trout often form shoals which swim away from the bottom, as did the experimental fish, and that aggressive behaviour within the shoals leads to the formation of social hierarchies. The dominant fish in these hierarchies are usually located at the head of the shoal and thus gain an advantage with respect to feeding, especially in obtaining food from organic drift in the stream. (Yamagishi, 1962)

In general terms, then, the function of aggression could be described as the conferring of an advantage upon dominant individuals, allowing them to succeed, for instance in defending a territory or obtaining food, at the expense of subordinate fish.

As mentioned above, the distribution of the fish in the tanks was similar to that in stream pools and aggression in the experimental fish led to the establishment of at least partial hierarchies. There is a difference between the natural and experimental situations, though, in that, because of the method of introduction of food dominance in the tanks conferred no advantage in feeding, nor in any other respect. This difference is most important as the lack of an advantage associated with dominance means that the aggression in the tanks was effectually divorced from any real function. In turn, the lack of an appreciable function of aggression in the experimental situation eliminates the possibility of function-achievement as the process of aggression reduction by availability of cover, and brings the discussion back to its virtual starting point.

Aggressive behaviour in captive fish is affected by parameters other than the topography of the environment. Density of the fish is important in this respect (SE2) but other, less obvious, factors can also influence levels of aggression. Working with Atlantic salmon, Symons (1968) showed that groups of juvenile fish responded to deprivation of food by
strengthening social hierarchies, a result of increased aggression, especially of dominant fish. If an environment without food is regarded as unfavourable, Symons' results could be interpreted as meaning that an unfavourable, or stressful environment brings about increased aggression.

In the present experiment the control condition although providing sufficient food and having water of adequate quality may have been unfavourable for the trout because of the absence of any form of escape route from potential predators. Some of the experimental conditions did provide possible means of escape and may, therefore, have given the fish a greater degree of 'security' in their environment.

There is no real evidence that a stressful or 'insecure' environment stimulates high levels of aggression in trout but some circumstantial evidence and a lack of alternatives point to the tentative conclusion that the tunnels and banks reduced aggression by creating a less stressful environment for the groups of fish.

To summarise, it is evident that the aggressive behaviour of juvenile trout is affected by many factors, including the complexity of the environment as produced by the structures used in this experiment. The experiment was designed to establish whether or not different types of structure would produce different effects upon aggression and this object was achieved, with the results demonstrating clear differences in the effects of the four structure types. However, whilst the data allowed the demonstration of these different effects, they did not permit a full analysis of the processes by which these effects, and the differences, were brought about and consequently much of the discussion is of necessity based upon conjecture.
1.6

Analysis of the Wigwag Display

1.6.1

Introduction During the second large-tank experiment of BE3, a form of aggressive behaviour not seen in earlier experiments was observed and was recognised as the wigwag display described by Hartman (1965) in coho salmon and steelhead trout and by Jenkins (1969) in brown trout.

In the present experiments, the wigwag display was seen in all groups of fish used and made up a small but consistent part of the total aggressive behaviour. As the display occurred repeatedly in very similar situations and was performed by both dominant and subordinate individuals, it was decided to study the display in an attempt to discover its role in the aggressive relationships amongst the fish.

1.6.2

Materials and Methods Records on the wigwag display were kept for the last three experimental runs of BE3, large-tank second experiment. A full description of the methods and apparatus used in the large-tank experiment of BE3 is given in Sections 1.5.5 and 1.5.8.

Each time a wigwag display was seen, the following data were recorded, using a portable tape recorder: a) the fish involved, either a dominant and a subordinate (termed alpha and beta respectively) or two subordinates; b) the fish which performed the display; c) whether the display was performed with the head up, down or on an even keel; d) the behaviour of the involved fish immediately before the display; e) the behaviour of the involved fish immediately after the display and f) the direction of the display relative to the displayed-to fish. Records were kept for all groups of fish. At the end of each day's observations data on the wigwag were transferred to record sheets to permit analysis.
Results  
Because of the low incidence of wigwag displays, 1.49% of the total number of aggressive acts, the data for the three experimental runs were combined.

a) Description of Wigwag Display

The wigwag display was characterised by an extension of the fine, accompanied by exaggerated swimming movements. Wigwag displays were performed with the body horizontal or inclined, with the head up or down. At all body inclinations the longitudinal axis of the fish was slightly concave. The lower jaw and operculae were often, though not invariably, extended. Erection of the fine was dependent on the intensity of the display, except in the 'head-up wigwag', when the dorsal fin was slightly compressed. The 'head-up' position was similar to that seen in juvenile brown trout by Kalleberg (1958) and described by Jones and Ball (1954) as a dominance posture in spawning brown trout.

Individual displays lasted from 0.8 to 1.5 seconds, with between 4 and 7 tail-beats occurring in this time.

No differences were detectable between the displays performed by dominant (alpha) and subordinate (beta) fish.

The basic components of the wigwag bore a strong resemblance to those of the lateral threat, the main difference being the inclination of the body and the accentuated tail-beats of the wigwag. Another slight difference was seen in the angle of the pectoral fins; in the lateral threat, the pectorals were held almost vertically downwards with their width perpendicular to the length of the fish, as in the braking action of a swimming fish; when performing the wigwag, the pectoral fins tended to be held more in a horizontal plane, with their width parallel to the length of the fish. This positioning of the pectorals was possibly an adaptation to maintain the inclination of the body during the display.
b) Analysis of the Display

Wigwag displays were performed by both alpha fish and beta fish, allowing the data to be split into three categories according to which types of fish were involved and which fish was displaying, viz:

i) alpha and beta, alpha displaying

ii) alpha and beta, beta displaying

iii) two betas, in this category, the fish performing the display was always referred to as beta-2 and the displayed-to fish as beta-1.

i) Alpha and beta, alpha displaying

The 159 displays in this category accounted for 24.4% of the total observed and made up 60.2% of the displays involving fish of different social rank. A complete classification of the displays is given in Table 1.6.

It can be seen that in 89.3% of the displays observed, the wigwag of alpha fish were elicited by aggressive behaviour of beta fish, with a further 4.4% following mutual lateral threats. The most frequent beta-display evoking an alpha wigwag was the frontal threat, causing 62.9% of the displays.

The wigwag display by the alpha fish ended 24.5% of the interactions, with the fish separating.

In the majority of cases, 72.9% the wigwag was followed by another aggressive act by the alpha fish towards beta, which either submitted or fled. The more direct types of aggression were used in this situation, especially the nip (50.9% of total acts by alpha after wigwag) and the frontal threat/nip (29.3% of total acts by alpha after wigwag). As all the wigwag performed by the alpha fish took place in a direction away from the beta fish, the continued aggression meant that the alpha fish had to stop performing the wigwag and turn before continuing the interaction. When the fish separated immediately after the wigwag, turning did not take
### TABLE 1.6

Behavioural Components of Wigwag Displays Performed in the Category 'Alpha and Beta, Alpha Displaying'.

a) **Total Number of Wigwags Observed**

<table>
<thead>
<tr>
<th>Description</th>
<th>No.</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>159</td>
<td></td>
</tr>
</tbody>
</table>

b) **Angle of Body**

<table>
<thead>
<tr>
<th>Description</th>
<th>No.</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head up</td>
<td>19</td>
<td>11.9</td>
</tr>
<tr>
<td>Even keel</td>
<td>37</td>
<td>23.3</td>
</tr>
<tr>
<td>Head down</td>
<td>103</td>
<td>64.8</td>
</tr>
</tbody>
</table>

c) **Relative Occurrence of Components Preceding and Following Wigwag**

<table>
<thead>
<tr>
<th>Description of Component</th>
<th>Occurrence as a Preceding event</th>
<th>Occurrence as a Following event</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>%</td>
</tr>
<tr>
<td>Mutal Lateral Threat</td>
<td>7</td>
<td>4.4</td>
</tr>
<tr>
<td>Frontal Threat by Alpha</td>
<td>3</td>
<td>1.9</td>
</tr>
<tr>
<td>Frontal Threat by Beta</td>
<td>100</td>
<td>62.9</td>
</tr>
<tr>
<td>Lateral Threat by Alpha</td>
<td>2</td>
<td>1.3</td>
</tr>
<tr>
<td>Lateral Threat by Beta</td>
<td>12</td>
<td>7.5</td>
</tr>
<tr>
<td>Nip by Alpha</td>
<td>3</td>
<td>1.9</td>
</tr>
<tr>
<td>Nip by Beta</td>
<td>19</td>
<td>11.9</td>
</tr>
<tr>
<td>Chase by Alpha</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chase by Beta</td>
<td>6</td>
<td>3.8</td>
</tr>
<tr>
<td>Front-Threat/Nip by Alpha</td>
<td>2</td>
<td>1.3</td>
</tr>
<tr>
<td>Front-Threat/Nip by Beta</td>
<td>5</td>
<td>3.1</td>
</tr>
<tr>
<td>Nip/Chase by Alpha</td>
<td>1</td>
<td>0.6</td>
</tr>
<tr>
<td>Nip/Chase by Beta</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fish Separate</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
Aggression by the beta fish after an alpha wigwag took place on only four occasions (2.6%), and consisted of one nip and three frontal threats.

ii) Alpha and beta, beta displaying In this category, the situation was the opposite of that in section i) above, in that a low-ranking fish (beta) was performing the wigwag to a higher ranking fish. This type of interaction made up 16.2% of the total and was the least frequently observed.

Of the 105 beta wigwags, 101 (96.2%) were elicited by an aggressive act by the alpha fish with a further 2.9% resulting from mutual lateral threats. The most common aggressive act by alpha in this respect was the nip (41%).

After the wigwag, the fish separated in 39% of the cases and further aggression was shown by beta in 6.7% of the interactions. Further aggression by alpha fish made up 53.4% of the post-wigwag events, a much higher proportion than for the alpha wigwag.

All but one of the beta wigwags were performed away from the alpha fish. The exception occurred in response to alpha nipping beta, with beta then performing a head-up wigwag towards alpha. Alpha responded to this display by a frontal threat and nip towards beta.

The complete data are given in Table 1.7.

iii) Two betas, beta-2 displaying Wigwags were most frequently seen in situations involving two beta fish (59.4% of all wigwags).

From Table 1.8 it can be seen that 92.5% of the beta-2 wigwags were performed in response to aggressive acts by beta-1, the more common of these being the frontal threat (42.9%) and the nip (37.9%). Mutual lateral threats preceded a further 3.4% of the beta-2 wigwags.
### TABLE 1.7

Behavioral Components of Wigwag Displays Performed in the Category 'Alpha and Beta, Beta Displaying'.

**a) Total Number of Wigwags Recorded**

<table>
<thead>
<tr>
<th></th>
<th>No.</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>105</td>
<td></td>
</tr>
</tbody>
</table>

**b) Angle of Body**

<table>
<thead>
<tr>
<th></th>
<th>No.</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head up</td>
<td>11</td>
<td>10.5</td>
</tr>
<tr>
<td>Even keel</td>
<td>10</td>
<td>9.5</td>
</tr>
<tr>
<td>Head down</td>
<td>84</td>
<td>80.0</td>
</tr>
</tbody>
</table>

**c) Relative Occurrence of Components Preceding and Following Wigwag**

<table>
<thead>
<tr>
<th>Description of Component</th>
<th>Occurrence as a Preceding event</th>
<th>Occurrence as a Following event</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>%</td>
</tr>
<tr>
<td>Mutual Lateral Threat</td>
<td>3</td>
<td>2.9</td>
</tr>
<tr>
<td>Frontal Threat by Alpha</td>
<td>32</td>
<td>30.5</td>
</tr>
<tr>
<td>Frontal Threat by Beta</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lateral Threat by Alpha</td>
<td>3</td>
<td>2.9</td>
</tr>
<tr>
<td>Lateral Threat by Beta</td>
<td>1</td>
<td>1.0</td>
</tr>
<tr>
<td>Nip by Alpha</td>
<td>43</td>
<td>41.0</td>
</tr>
<tr>
<td>Nip by Beta</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Chase by Alpha</td>
<td>5</td>
<td>4.8</td>
</tr>
<tr>
<td>Chase by Beta</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Frontal Threat/Nip by Alpha</td>
<td>14</td>
<td>13.3</td>
</tr>
<tr>
<td>Frontal Threat/Nip by Beta</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nip/Chase by Alpha</td>
<td>4</td>
<td>3.8</td>
</tr>
<tr>
<td>Nip/Chase by Beta</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fish Separate</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
### TABLE 1.8

Behavioural Components of Wigwag Displays Performed in the Category 'Two Betas, Beta-2 Displaying'.

a) **Total Number of Wigwag Observed**

| Description of Component | Occurrence as a Preceding event | Occurrence as a Following event |
|--------------------------|---------------------------------|---------------------------------
| No. | % | No. | % |
| Mutal Lateral Threat | 13 | 3.4 | 1 | 0.3 |
| Frontal Threat by Beta-1 | 153 | 39.5 | 6 | 1.6 |
| Frontal Threat by Beta-2 | 3 | 0.8 | 18 | 4.7 |
| Lateral Threat by Beta-1 | 9 | 2.3 | 2 | 0.5 |
| Lateral Threat by Beta-2 | 1 | 0.3 | 1 | 0.3 |
| Nip by Beta-1 | 135 | 34.9 | 22 | 5.7 |
| Nip by Beta-2 | 8 | 2.1 | 61 | 15.8 |
| Chase by Beta-1 | 28 | 7.2 | 0 | 0 |
| Chase by Beta-2 | 2 | 0.5 | 2 | 0.5 |
| Frontal Threat/Nip by Beta-1 | 24 | 6.2 | 11 | 2.8 |
| Frontal Threat/Nip by Beta-2 | 2 | 0.5 | 43 | 11.1 |
| Nip/Chase by Beta-1 | 9 | 2.3 | 1 | 0.3 |
| Nip/Chase by Beta-2 | 0 | 0 | 7 | 1.8 |
| Fish Separate | – | – | 212 | 54.8 |

b) **Angle of Body**

- Head up: 29 (7.5%)
- Even keel: 66 (17.1%)
- Head down: 292 (75.2%)

---

*Note: This table provides a detailed analysis of the behavioural components observed during wigwag displays, focusing on the number of occurrences and their distribution among different categories.*
Separation occurred after 54.8% of beta-2 wigwag and further aggressive acts by beta-2 occurred after 34.1% of beta-2 wigwag. The balance, of 11.1%, representing occasions on which beta-1 performed further aggressive acts is intermediate between the values for the beta fish (2.5%) and the alpha fish (54.3%) in sections i) and ii) above.

Within the two betas category, a mutual head-down wigwag was observed on two separate occasions. Other variations were also noted. 'Circular wigwag' were seen three times and consisted of beta-2 swimming away from beta-1 on a curved path and eventually returning to face beta-1 after swimming in an almost complete circle whilst performing a head-down wigwag. Twice, wigwages were performed facing beta-1, once with beta-2 remaining stationary and once with beta-2 approaching beta-1. The only instance of a wigwag being used as a display initiating an aggressive interaction was recorded between two betas and resulted in beta-1 submitting.

All other wigwages were performed away from beta-1.

iv) Combined results If the data of the three categories are combined, a more general impression of the wigwag display is obtained. The most frequently observed type was the head-down wigwag (73.6% of all displays). Displays performed on an even keel, distinguished from the lateral threat by the amplitude of the tail-beats, accounted for 17.4% of the total and the remaining 9.0% of the displays were performed in the head-up position.

For the direction of the display, relative to the displayed-to fish, 98.7% of all wigwages were performed with the displaying fish moving away from the other fish involved. Other directions seen included mutually performed displays, 'circular wigwage' and wigwages towards the displayed-to fish.

Of all wigwages, 92.3% were performed in response to an aggressive act by
another fish. A further 3.5% developed from mutual lateral threats. In 4.2% of the cases observed the fish performing the wig wag initiated the aggressive interaction.

The behavioural events immediately following wigwags were split into three types. The wig wag was the last act of the aggressive interaction in 44.9% of the total. Further aggression by the fish performing the wig wag accounted for 39.3% of the total. Further aggression by the displayed-to fish was recorded for 15.8% of the total, including 8.8% by alpha fish after beta wigwags.

59.4% of all wigwags were performed between fish of apparently equal social rank (two betas category) and 40.6% involved fish of different social ranks. Of the wigwags performed in different-rank situations, 60.2% were by the higher ranked fish.

1.6.4 Discussion

In the majority of aggressive interactions in juvenile brown trout the fish initiating the interaction appears to possess an advantage (the 'displacement privilege' of Jenkins, 1969) in that the fish being attacked almost invariably flees or exhibits a submissive posture. This advantage is strengthened if the initiator is socially dominant over the attacked fish, and retaliation in a dominant/subordinate interaction is an extremely rare event. Perhaps as a consequence of this, the majority of the aggressive behaviour patterns of the trout can be classified as offensive. The frontal threat, nip and chase are good examples of purely offensive acts. The lateral threat has a slightly ambiguous nature as it may be used in both offensive and defensive situations. The immediate impression gained from the wig wag, though, is that it is a very specialised display used exclusively in defensive situations.

To qualify as defensive, any display must be performed only in response to aggressive behaviour by another individual. The wig wag so qualifies
as it is elicited in 92.3% of the cases observed by aggression by the
other fish involved. The low overall frequency of occurrence of the
wigwag compared with other forms of aggression also suggests that it has
a highly specific function.

Assuming, then, that the wigwag is primarily a defensive display, what
are the factors governing its effectiveness? If a defensive display is
to be successful it must result in the initiator of the interaction
showing no further aggression. Of the events immediately following the
wigwag display, two of the three types observed may be considered as the
outcome of a successful defence. If the two fish involved separate with
no further aggression, or if there is further aggression by the fish
performing the wigwag, then the defensive display was effective. If
further aggression by the displayed-to fish follows the performance of
the wigwag, the defence was ineffective.

From the data obtained, a measure of the effectiveness of the wigwag as
a defence can be calculated by summing the percentage occurrence of the
two 'successful' types of post-wigwag events. For the combined results
the wigwag was 84.2% effective. When the effectiveness of the wigwag is
calculated for the fish-involved categories, it can be seen that the
social ranking of the fish involved had a strong influence on the
effectiveness of the display. With alpha and beta involved and alpha
displaying, the wigwag was 97.4% effective but with the same fish involved
and beta displaying, the effectiveness was 45.7%. When two betas were
involved the effectiveness of the wigwag was 88.9%.

A discussion of the effect of social rank upon the effectiveness of the
defensive properties of the wigwag display must take into consideration
the relative frequencies of other forms of aggressive behaviour between
fish of the same or different social ranks. In the groups of fish in this
experiment, the alpha fish maintained their dominant positions by being
the most aggressive fish of the groups. Within each group the dominant
fish was likely to have been responsible for between 55 and 65% of the total aggressive acts. The remainder of the aggression was mostly between beta fish with a very low proportion, probably less than 2% of the total, composed of attacks on alpha by beta. These figures are estimates based on observation and results from previous experiments; no records were kept on the relative performance of aggressive acts by different-ranked fish in this experiment.

The information shown in Table 1.9 may be calculated assuming that the estimates of the relative performance of aggressive behaviour by the different social ranks are of the correct order.

From Table 1.9 it can be seen that when alpha is attacked by beta, the wigwag display is performed in a relatively high percentage of cases. In actual instances of beta/alpha aggression observed during this experiment, the most frequent response of alpha was either to perform an intense frontal threat to beta, or to repeatedly nip and chase it.

Further from Table 1.9, it is apparent that a beta fish is much more likely to perform a wigwag display in response to aggression from another beta than from an alpha fish. This difference suggests that beta fish are somehow aware of the aggressive superiority of alpha fish and are consequently reluctant to perform a defensive display. The low effectiveness of the beta/alpha wigwag that are performed may further inhibit any defence by the beta fish.

In an aggressive interaction involving two fish of different social ranks, (alpha and beta) it seems that the rank of the initiator of the interaction largely determines whether or not a wigwag will be performed, and, if it is performed, whether or not it will be successful as a defence.

If the initiator is an alpha fish, the attacking-advantage is reinforced by its higher social rank. Retaliation is most unlikely, and if a defensive display is given, it is likely to be ineffective. If a beta
### TABLE 1.9

Relative Performance of Wigwag Displays and Other Components of Aggressive Behaviour.

| Number of Non-Wigwag Aggressive Acts Observed | 43,010 |
| Number of Wigwag Displays Observed | 651 |
| Total Number of Aggressive Acts Observed | 43,661 |

<table>
<thead>
<tr>
<th>Ranks Involved and Direction</th>
<th>Occurrence as % of Total</th>
<th>Estimated Number of Non-Wigwag Acts Elicited by Aggressive Acts Eliciting Wigwag</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpha Beta</td>
<td>60</td>
<td>25,806 101 0.39</td>
</tr>
<tr>
<td>Beta Beta</td>
<td>38</td>
<td>16,344 359 2.19</td>
</tr>
<tr>
<td>Beta Alpha</td>
<td>2</td>
<td>860 141 16.40</td>
</tr>
<tr>
<td>TOTALS</td>
<td>100</td>
<td>43,010 600* TOTALS</td>
</tr>
</tbody>
</table>

*This total is less than the total number of observed wigwages because it does not include those wigwages which followed an aggressive act by the fish performing the display.
fish initiates an interaction against an alpha fish, then retaliation, in the form of offensive aggressive behaviour, is much more probable as the higher social rank of the attacked fish balances or outweighs the attacking-advantage. Any defence in this situation will almost certainly be effective.

When two fish of apparently equal rank are involved in an aggressive interaction, as in the two-betas category, the interpretation of the relationship between social rank and the performance and effectiveness of the wigwag display is more speculative. This is because the fish are of socially equal ranks only as far as the observer is concerned.

The similar appearance and behaviour of the beta fish in the groups used in this experiment suggested that all betas were on the same social level, but it is possible that further social stratification of the subordinate fish, caused by differences in aggressive capability, was actually the case.

If the groups of subordinates were socially stratified, it would be expected that the total number of aggressive acts would be comprised of both interactions initiated by the higher-ranked fish (down-grade interactions) and interactions initiated by the lower ranked fish (up-grade interactions). It might also be expected that the majority of interactions would be down-grade, as was observed between alpha and beta fish. However, because the distinction between ranks within the groups of subordinate fish would probably be less pronounced than between alpha and beta fish, up-grade interactions would perhaps occur more frequently than in true alpha/beta situations.

If the estimates obtained in Table 1.9 of the relative occurrence of wigwag in the different rank-involved categories are accepted as reliable, it is possible to calculate the relative frequency of up- and downgrade interactions within the two-betas category, as follows:
Let there be 100 beta/beta interactions.

Of these, let \( x \) = Number of upgrade interactions

let \( y \) = Number of downgrade interactions

Thus, \( x + y = 100 \) .........................................................(1)

From the 100 interactions, the expected number of wigwag is 2.19 (from Table 1.9).

These wigwag will be made up of downgrade wigwags, elicited by the \( x \) upgrade interactions, and of upgrade wigwags, elicited by the \( y \) downgrade interactions.

Estimated percentage occurrence of wigwage in observed interactions was 16.40% in upgrade and 0.39% in downgrade interactions.

So, Expected Number of upgrade wigwage is given by 0.0039\( y \),

and Expected Number of downgrade wigwage is given by 0.1640\( x \).

Thus, \( 0.1640x + 0.0039y = 2.19 \) .........................................................(2)

The simultaneous equations (1) and (2) are solved in the usual way to give:

\[
\begin{align*}
x &= 11.24 \\
y &= 88.76
\end{align*}
\]

As the original number of interactions was 100, this means that in the beta/beta category, 88.76% of the interactions were downgrade, and 11.24% were upgrade.

Using these values of the relative occurrence of up- and downgrade interactions, it is now possible to calculate the relative occurrence of up- and downgrade wigwage in the beta/beta category, thus:

Let there be 100 beta/beta interactions.

Of these, 11.24 will be upgrade interactions and

88.76 will be downgrade interactions and there will
be 2.19 wigwags.

Using the estimates of occurrence of up- and downgrade wigwag as in the previous calculation:

Number of downgrade wigwag = 0.1640x
Number of upgrade wigwag = 0.0039y

As x and y are known, the actual numbers of down- and upgrade wigwag are 1.8436, and 0.3464, respectively.

Percentage occurrence of wigwag is given by:

i) upgrade, $\frac{0.3464}{2.19} \times 100 = 15.82\%$

ii) downgrade, $\frac{1.8436}{2.19} \times 100 = 84.18\%$

The validity of these calculations can now be checked by performing a third calculation, based on observed data only, to give the relative occurrence of up- and downgrade wigwag.

The third calculation is carried out as follows:

Let there be 100 beta/beta wigwags.
Let a = Number of upgrade wigwag.
Let b = Number of downgrade wigwag.
Thus $a + b = 100$ .................................................................(3)

Observed efficiency for upgrade wigwag = 45.7%
Observed efficiency for downgrade wigwag = 97.4%

So, Number of effective upgrade wigwag is given by

$0.457a$

and Number of effective downgrade wigwag is given by

$0.974b$

Observed effectiveness of beta/beta wigwag is 88.9%.

Assuming that up and downgrade wigwag within the beta/beta category have the same efficiencies as those observed between alpha and beta, then

$0.457a + 0.974b = 88.9$ .........................................................(4)
Solving the simultaneous equations (3) and (4) gives

\[ a = 16.45 \text{ and } b = 83.55. \]

The obtained values of \( a \) and \( b \) compare very closely with the figures obtained in the previous calculation, viz. 16.45 and 83.55 of 15.82 and 84.18. This close agreement between the values for upgrade and downgrade wigwag occurrence within the beta/beta category of interactions obtained from observed and estimated data suggest that the estimates used were of the correct magnitude.

The fact that the above calculations can be performed supports the idea that there was social stratification within the groups of beta fish. However, there was no direct evidence of a linear hierarchy. When observing the groups of fish it was always extremely easy to identify the alpha fish, but social distinction between various beta fish was almost impossible, although recognition of individual beta fish was possible in most groups and occasionally highly aggressive beta fish were seen.

The contradiction between inferences from calculated data and observed data may be partially explained by considering the plasticity of an individual fish's social status. Various workers with trout and other salmonids have shown that, if the dominant fish is removed from a group, its social position is filled by one of the former subordinates, usually the largest (eg. Stringer and Hoar, 1955). Similar observations have been made on many other fish, mostly territorial, but including some species, eg. tench (Barrow, 1955) not generally thought of in this way.

In the groups of fish used in this experiment, then, each beta fish may be regarded as a potential alpha. However, the presence of the dominant fish has an inhibitory effect upon the aggressive behaviour of the subordinates, preventing them from attaining their full social potential. Such inhibition of subordinate aggression may also serve to reinforce the dominance of the alpha fish and so reduce the need for continual
reassertion of dominance through aggressive interactions.

If the dominant fish of a group were removed, one of the beta fish would quickly assume the alpha role. Obviously, only one of the group of subordinates could become the new dominant and it would be expected that the most aggressive beta would succeed. Were this new dominant removed, it would again be replaced by the most aggressive of the remaining subordinates, and so on until only two fish were left. The mechanism governing the sequence in which the various subordinates would assume dominance must be the maximum aggressiveness of each fish. This means that although the beta fish were all apparently of the same social rank, there was most probably a linear ranking of their aggressive capacity.

The alpha-induced inhibition of aggression which prevents the subordinates from attaining their alpha potential similarly does not permit the expression of the potential linear hierarchy within the group of subordinates.

If the fish in a group were capable of individually recognizing the other group members and can assess each other's actual social status, as is suggested by the low incidence of upgrade interactions, there is no apparent reason why they should not be able to assess potential status. The actual status of each fish in a group is determined in the few hours after the formation of that group, or in this case the introduction of the fish to the tanks, by aggressive interactions. During this period of status determination, each fish has the opportunity of learning to recognize the other group members and of discovering by direct aggressive interaction which individuals are more, and which less aggressive than itself, and a linear hierarchy may be established. When the group structure has stabilised with the suppression of any linear hierarchy and all beta fish on apparently the same social level, individual recognition within the group of betas would maintain the hierarchy in a latent form.
The existence of such a latent hierarchy would account for the calculated composition of aggression within the subordinate group as it would operate in the same way as a true hierarchy by inhibiting upgrade interactions. The higher incidence of upgrade interactions in the beta/beta category than in the beta/alpha (11.24% cf 3.2%) may be a result of the very similar appearance of all the beta fish, in contrast to the very distinctive colouration and demeanour of the alpha fish. A latent but effective hierarchy would also result in the high observed effectiveness of beta/beta wigwags, as the majority would be downgrade and hence almost totally effective.

With absolute social equality amongst the members of the subordinate group it would have been expected that either there would have been no wigwag at all as the attacking-advantage of the fish initiating the interaction would have made it temporarily dominant, thus precluding defence, or that wigwags would have occurred in 50% of the interactions. Similarly, if there was no social distinction between subordinates the effectiveness of the wigwag would presumably have depended entirely upon chance and would have been expected to have had an average of 50%.

In conclusion, these observations have shown that the wigwag display as used in confined groups of juvenile brown trout is entirely defensive in context and is thus a refined display carrying a specific interpretation. Because of its similarity to the lateral threat, the wigwag could be regarded as an extension of, or as having evolved from, the lateral threat as it is used in a defensive situation. The actual performance of the display appears to be highly ritualised as its behavioural components are far removed from actual fighting behaviour.

The social ranks of the two fish involved in an aggressive interaction are a most important factor determining whether or not a wigwag display will be performed and also largely govern its effectiveness as a defence. Generally, the higher ranking fish is much more likely to perform a
wigwag in response to aggression from a lower ranking fish than vice versa and downgrade wigwags are much more likely to be effective than upgrade wigwags. Data from fish of apparently equal rank suggest that there may be a latent linear hierarchy within the group of subordinate fish which affects the performance and the effectiveness of the wigwag display.
2. EXPERIMENTS ON THE EFFECT OF ENVIRONMENTAL COMPLEXITY UPON ENVIRONMENTAL CARRYING CAPACITY
2.1

Introduction

Many of the contributions to the literature concerning the carrying capacity of salmonid habitats have suggested that complex environments are capable of supporting larger resident populations than simple ones, e.g. Saunders and Smith (1962); Elser (1968); Lewis (1969); Bjornn (1971) and Hunt (1971).

The importance of aggressive behaviour and dominant/subordinate relationships in determining the size of salmonid populations has been shown both in streams (Onodera, 1962) and stream-tanks (Chapman, 1962). For brown trout fry, Le Cren (1972a) suggested that food-linked territoriality was a major population-limiting mechanism.

The present experiments were performed to investigate the possible relationships among environmental complexity, aggressive behaviour and carrying capacity for juvenile brown trout. Three experiments were carried out. In the preliminary experiment one method of assessing carrying capacity was tested. This data was used as a basis for the design of the subsequent experiments. The second experiment confirmed that complexity did influence carrying capacity and the final experiment attempted to analyse the relationship between aggressive behaviour and carrying capacity in environments of varying complexity.

2.2

Preliminary Carrying Capacity Experiment

2.2.1

Materials and Methods

The equipment used in these experiments is described in Section 4 of the Appendix.

Channel 1, representing a simple type of environment was left with the floor bare whilst the other, Channel 2, was provided with coarse gravel and large and small stones, 10-15cm in size, representing a complex type
of environment. Water depth in Channel 1 was 15.2 cm immediately below
the upstream dam and 13.7 cm immediately above the downstream dam. In the
other channel the depth varied according to the substrate and varied from
6.2 - 14.5 cm. Channel 2 was divided into three sections of approximately
equal length, the upper and lower thirds being relatively deep (10-14 cm)
with the central third being much shallower (6-8 cm).

Two experimental runs were carried out in the preliminary series, each
being performed in the same way. An initial population of six brown trout
fingerlings was placed in each channel. For the first two days any emigrant
fish were returned to the channels and from day 3 to day 7 emigrants were
removed and measured, the traps being searched once daily. From day 8
onwards fish were introduced at the rate of one per channel per day until
the end of the experiment. Immigrant fish were measured and introduced to
the upstream end of the channel after the second feeding. As far as was
possible, the immigrant fish for each channel for any one day were chosen
to be approximately equal in size. Emigrant fish were removed and
measured.

The fish were fed twice daily, once in the upstream end of the channel
and once in the downstream end to avoid any feeding advantage to a fish
in one of these positions. At each feeding food pellets were introduced
for a period of two minutes after the first fish fed, at a rate which
ensured that there was no accumulation of uneaten food.

As each channel was identical in size, water supply, initial population
size and feeding routines, any significant differences in the final
population sizes would be attributable to the differences in the topography
of the two channels. During the experiment the resident population for
any particular day was taken as the number of fish in the channel
immediately prior to the introduction of the immigrant fish. The final
population size was taken as the number of fish resident in the channel.
after a fixed period of time. In the first preliminary experiment this period was 50 days and in the second run 34 days.

It was thought that the populations in each type of environment would reach an optimum size after which time the rates of immigration and emigration would be equal.

2.2.2

Results

a) First run— By the seventh day the initial population of six fish remained in Channel 2, the complex environment. The population in Channel 1, the simple environment, had decreased to two fish, with equal numbers of upstream and downstream emigrants. The fish emigrating upstream were noticeably larger than those emigrating downstream, their lengths being 72 and 76, and 68 and 66mm respectively. Upstream emigrants were of similar length to the dominant fish which remained in Channel 1.

The results for this run are shown in Figure 2.1. The difference between the environment types is immediately apparent. Whilst the population remained almost constant at two fish in Channel 1, the population of Channel 2 increased and showed no signs of levelling off.

Each channel received 29 immigrants. All immigrants left Channel 1 but 12 stayed in Channel 2, accounting for the increase in population. Of the 29 emigrants from Channel 1, 23 left within one day of introduction. The others stayed between three and six days. In Channel 2, five of the 17 emigrants left within one day, the other 12 leaving after periods of up to eight days. The average period of residence for an immigrant to Channel 1 was 1.48 days and for an immigrant to Channel 2 was 2.73 days.

In both environment types most of the emigrants were found in the downstream trap; 73% for Channel 1 and 82% for Channel 2.

During the experiment the fish were observed for short periods of time and records kept of their behaviour and distribution. Strictly comparable
Fig 2.1  Resident populations of juvenile brown trout in environments of different complexity
Initial populations 6 fish
1 immigrant per day from day 7
Emigrants removed daily
△△△ Simple environment  ▲▲▲ Complex environment
records were not obtained because of the difference in population size between the two channels, therefore no rigid method of observation was followed.

At all times in both channels a single dominant fish was seen, easily identified by being larger and paler than the subordinate fish. Immigrants larger than the resident were introduced but emigrated in one or two days, supporting the suggestions of Miller (1958) and Chapman (1962) that prior residence confers a social advantage. In Channel 1 only two fish were present during most of the observation periods and were usually stationed on the bottom, 5-10cm in front of the downstream dam, facing upstream with the subordinate fish lying just behind the dominant. If the subordinate moved in front of the dominant it was invariably attacked and chased around the channel until the original positions were resumed.

As there were more fish in Channel 2, distribution of the fish was harder to monitor than in Channel 1 as fish were more difficult to identify individually. Also, their cryptic colouring was very effective in this 'natural' environment making it awkward to see the whole population at once. Generally most of the fish were found together in a loose shoal in the downstream third of the channel. It was noticeable that the dominant maintained its position at the head of the shoal, just upstream of a group of large stones. As in Channel 1, the dominant attacked any subordinate which ventured in front of it, the ensuing chases often continuing for up to 50 seconds.

During feeding, the shoal in Channel 2 broke up and the fish became highly active whilst food was available. Immediately after feeding there was a high level of aggression in Channel 2, which gradually decreased as the shoal reformed.

On several occasions in both channels fish were seen crossing the dam into the traps. In all cases of downstream emigration the emigrant fish
were subordinates that were being actively pursued by the dominant and were therefore 'chased out' of the channel. Upstream emigrants were usually subordinates being chased but on rare occasions single fish were seen to leap the dam with the dominant taking no part. When they had left the channels it was possible for emigrant fish to re-enter and fish were seen crossing both up- and downstream dams into the channels.

A difference between the behaviour of the dominant fish in the two environments was noticed when immigrant fish were introduced. In Channel 1 each new fish was immediately attacked and chased by the dominant fish whereas the dominant in Channel 2 swam up to the immigrant and 'inspected' it before ignoring it completely as it settled on the bottom in the group of subordinates behind the dominant. This difference could have been the result of either the Channel 1 dominant being simply a much more aggressive individual than the Channel 2 dominant, or as a consequence of the way in which the environment type affects aggressive behaviour.

b) Second run: In both channels the initial populations of six fish had decreased by the seventh day. Channel 1 had only one resident fish, there having been three upstream and two downstream emigrants. In Channel 2 two fish were resident with equal numbers of up- and downstream emigrants. The emigrants in this run did not show the difference in size with direction of emigration that was noticed in the first run. Upstream emigrants for Channels 1 and 2 measured 70, 65, 70 and 70, 65 mm respectively and downstream emigrants measured 70, 63 and 72, 61 mm respectively. The largest fish remained in Channel 1 and the largest and second smallest remained in Channel 2.

After the introduction of immigrants had started the populations remained stable. Channel 1 fluctuated between one and two residents and Channel 2 contained five fish for most of the experiment. The progress of the populations is shown in Fig. 2.2. Compared with the first run the population of Channel 2 was much more stable and much smaller. This may
Fig 2.2 Resident populations of juvenile brown trout in environments of different complexity
Initial populations 6 fish
1 immigrant per day from day 7
Emigrants removed daily
△△△ Simple environment  ▲▲▲ Complex environment
reflect differences in individual fish's aggression.

In this run 20 immigrants were introduced to each channel. In both channels the original dominant was found to emigrate after the introduction of a larger immigrant. For Channel 1, an 80mm immigrant caused the resident dominant of 73mm to emigrate three days later and in Channel 2 a 76mm immigrant ousted the 74mm resident dominant after two days. Both resident dominants emigrated downstream.

The majority of emigrations were in a downstream direction. In Channel 1, 65% of the total emigrations were downstream and in Channel 2, 53%. The downstream majority was lower in this run than in the previous one.

Behavioural observations were made from the introduction of the initial populations until approximately half-way through the run. For each 10-minute period of observation the time since feeding and number of residents present was noted as well as the total number of aggressive acts. For any pair of observations the time since feeding in each channel was the same. The number of aggressive acts per fish per hour were calculated for each channel. (This is not a particularly good method of monitoring aggression as most of the aggression was performed by the single dominant fish but the data does give some indication of the intensity of aggression.) These results are shown in Table 2.1.

The observed aggression in Channel 2 was much higher than might have been expected. The reason for this was not obvious but on several occasions the fish in Channel 2 were seen to behave in an unusual manner. For example on 14.12.73 with three fish in the channel, the number of aggressive acts per fish per hour was 198 for the first observation period, more than four times the aggression for Channel 1, also with three fish at that time. Whilst the fish in Channel 1 were spread out over the whole of the available area those in Channel 2 stayed close together in an area of about 0.1m², constantly fighting. As this observation was made soon
TABLE 2.1
Aggressive behaviour of juvenile brown trout in the second run of the
preliminary carrying capacity experiment.

<table>
<thead>
<tr>
<th>Date Dec.</th>
<th>Number Fish</th>
<th>Total No. Aggressive Acts</th>
<th>Aggressive acts per fish per hour</th>
<th>Number Fish</th>
<th>Total No. Aggressive Acts</th>
<th>Aggressive acts per fish per hour</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 1973</td>
<td>6</td>
<td>41</td>
<td>41</td>
<td>5</td>
<td>83</td>
<td>100</td>
</tr>
<tr>
<td>11</td>
<td>5</td>
<td>90</td>
<td>108</td>
<td>6</td>
<td>72</td>
<td>72</td>
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<tr>
<td>12</td>
<td>4</td>
<td>51</td>
<td>77</td>
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<td>46</td>
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<td>12</td>
<td>3</td>
<td>25</td>
<td>49</td>
<td>6</td>
<td>26</td>
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</tr>
<tr>
<td>13</td>
<td>6</td>
<td>98</td>
<td>98</td>
<td>6</td>
<td>57</td>
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</tr>
<tr>
<td>14</td>
<td>3</td>
<td>24</td>
<td>48</td>
<td>3</td>
<td>99</td>
<td>198*</td>
</tr>
<tr>
<td>14</td>
<td>2</td>
<td>00</td>
<td>00</td>
<td>2</td>
<td>00</td>
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<tr>
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<td>--</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>18</td>
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<td>--</td>
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<td>1</td>
<td>--</td>
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<td>1</td>
<td>--</td>
<td>--</td>
<td>3</td>
<td>61</td>
<td>122*</td>
</tr>
<tr>
<td>24</td>
<td>1</td>
<td>--</td>
<td>--</td>
<td>3</td>
<td>15</td>
<td>30</td>
</tr>
</tbody>
</table>

The total aggression scores are the numbers of aggressive acts recorded
in ten-minute observation periods. For each pair of results, observations in each channel were made at equal times after feeding.

Numbers of fish given here do not correspond exactly to the populations
in Fig. 2 because of emigration and re-immigration taking place after the
observation periods and before the population counts.

*See text
after the start of the experiment it may have been that these three fish were equally matched individuals competing for possession of a territory based at the place where they were fighting. Subsequent to this particular observation the population declined to two fish for the other two observation periods on this date, with aggressive scores of 0 and 6 aggressive acts per fish per hour. This suggests that the ownership of the disputed territory may have been settled by the emigration of one fish and the establishment of a dominant/subordinate relationship between those remaining.

Later in the run the dominant fish in Channel 2 had apparently taken the whole of the channel as its territory and patrolled the area, repeatedly following the same route, each 'round trip' lasting 30-45 seconds, followed by up to two minutes resting in one of two stations. Any subordinates noticed on route were usually attacked but were sometimes ignored. As the population increased in Channel 2 the size of the dominant's territory decreased to about 3 of the channel area with the subordinates lying behind the dominant. At one point (24.12.73) with three fish present a subdominant took up a territory behind that of the dominant and the high aggression of 122 acts per fish per hour resulted from the single subordinate repeatedly being chased from one territory to the other.

2.2.3 Discussion

The results of the preliminary experiment strongly suggest that the complexity of an environment influences its carrying capacity, with a complex environment (Channel 2) supporting larger resident populations.

Observations of actual emigrations, and apparent correlations between the aggressiveness of the dominant fish and the size of the resident population support the hypothesis that aggression is the process by which fish are 'forced' to emigrate.
Differences in results between the two runs, for instance in resident population size in Channel 2, or the effect of immigrants larger than the resident dominant, do not alter the basic inference concerning the relationship between environmental complexity and carrying capacity but indicate a need for a changed experimental procedure.

2.3

Second Carrying Capacity Experiment

2.3.1

Materials and Methods The equipment used in the secondary series of experiments was exactly the same as in the preliminary series. Channel construction, water flow-rates, photoperiod and feeding routines were retained completely. Experimental procedure was altered in order to decrease the time needed for each experimental run.

Instead of starting with a low initial density in the channels each channel was stocked with twenty fingerlings taken at random from the holding tanks. This number was based on the results of the preliminary series and was assumed to be in excess of the carrying capacity of either channel. After introduction of the fish, the up- and downstream traps were searched at 24-hourly intervals and any emigrants were removed and measured. The experimental run was terminated when the population in one of the channels had decreased to two fish.

Records of the aggressive behaviour of the fish were kept during this experiment. The number of aggressive acts was monitored for periods of five minutes immediately after feeding and the number of fish present was also noted.

2.3.2

Results As all three experimental runs were carried out in the same manner the results of each run will not be presented separately.
The duration of each run was short, the times from initial stocking to termination being 5, 4 and 8 days for the first, second the third runs respectively. To allow comparison of the three runs the raw data were treated to give the Mean Obtained Capacity for each channel in each run. Mean Obtained Capacity was given by the formula: 

\[ \text{MOC} = \frac{\sum_{i=1}^{n} P_i}{n} \]

where MOC = Mean Obtained Capacity, 

\[ P_i = \text{Resident population on day } i, \]

and \( n = \text{Number of days in experimental run}. \)

The raw data and derived MOC's are presented in Table 2.2. When analysed by a Two-Factor ANOVA the MOC data indicated that, at \( P = 5\% \), the 'natural environment' of Channel 2 had a significantly higher carrying capacity than the Channel 1 'artificial environment'. There was no significant effect of replicate upon carrying capacity.

The majority of emigrations were downstream. In Channel 1, 76% of all emigrants (taken over the three runs) were in a downstream direction and in Channel 2, 89%.

Behavioural observations were made twice daily in all of the experimental runs. Table 2.3 shows the results of the aggression monitoring for the three runs. There was an overall increase in the level of aggression with time. For runs 1 and 3 there were significant (\( P = 5\% \)) Product-Moment Correlation Coefficients for both channels between aggression and time (observation number). Run 2 was not analysed because of the low number of observations.

Levels of aggression in runs 1 and 3 were analysed by a Two-Factor ANOVA which indicated that, for run 1 there was a significant effect of environment type at \( P = 5\% \) and for run 3 there was an effect of environment type significant at \( P = 0.1\% \), and an effect of time (observation number) significant at \( P = 5\% \). In both runs aggression in Channel 1 was the higher.
TABLE 2.2
Results of the second carrying capacity experiment

RESIDENT POPULATION ON DAY 1

<table>
<thead>
<tr>
<th>DAY</th>
<th>n</th>
<th>Run 1</th>
<th>Run 2</th>
<th>Run 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>C1</td>
<td>C1</td>
<td>C1</td>
</tr>
<tr>
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</tr>
<tr>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td>18</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL*</td>
<td></td>
<td>44</td>
<td>69</td>
<td>85</td>
</tr>
<tr>
<td>FISH-DAYS</td>
<td></td>
<td>13.8</td>
<td>19.3</td>
<td>17.5</td>
</tr>
</tbody>
</table>

*For the calculation of MOC, 'Total Fish-Days' describes the term
\[ \sum_{i=1}^{n} P_i \] in the equation
\[ \text{MOC} = \frac{\sum_{i=1}^{n} P_i}{n} \]
**TABLE 2.3**

Aggressive behaviour of juvenile brown trout in the second carrying capacity experiment. Aggression expressed as aggressive acts per fish per hour. All observations made immediately after feeding.

<table>
<thead>
<tr>
<th>DAY</th>
<th>CHANNEL 1</th>
<th>CHANNEL 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>12.6</td>
<td>4.8</td>
</tr>
<tr>
<td>2</td>
<td>55.2</td>
<td>52.8</td>
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<tr>
<td>2</td>
<td>63.6</td>
<td>54.0</td>
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<tr>
<td>3</td>
<td>120.0</td>
<td>72.0</td>
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<tr>
<td>3</td>
<td>207.6</td>
<td>85.2</td>
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<tr>
<td>4</td>
<td>187.2</td>
<td>84.0</td>
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<tr>
<td>4</td>
<td>147.6</td>
<td>68.4</td>
</tr>
<tr>
<td>2</td>
<td>99.6</td>
<td>39.6</td>
</tr>
<tr>
<td>2</td>
<td>94.6</td>
<td>54.0</td>
</tr>
<tr>
<td>3</td>
<td>231.6</td>
<td>40.0</td>
</tr>
<tr>
<td>3</td>
<td>0.0</td>
<td>60.0</td>
</tr>
<tr>
<td>1</td>
<td>69.9</td>
<td>39.6</td>
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<td>1</td>
<td>69.6</td>
<td>34.8</td>
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<tr>
<td>2</td>
<td>58.8</td>
<td>42.0</td>
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<tr>
<td>2</td>
<td>82.8</td>
<td>56.4</td>
</tr>
<tr>
<td>3</td>
<td>86.4</td>
<td>54.0</td>
</tr>
<tr>
<td>3</td>
<td>92.4</td>
<td>56.4</td>
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<tr>
<td>4</td>
<td>114.0</td>
<td>62.4</td>
</tr>
<tr>
<td>4</td>
<td>122.4</td>
<td>60.0</td>
</tr>
<tr>
<td>5</td>
<td>175.2</td>
<td>86.4</td>
</tr>
</tbody>
</table>
Territorial behaviour was observed in both channels. In Channel 1, run 2, a subdominant fish had, by the second day, taken up a partial territory in the surface 2-3 cm in a corner made by the upstream dam and the side of the channel. Although the holder of this territory drove away subordinates from its station it was unable to repel the dominant fish which frequently attacked it. When attacked by the dominant the subdominant fled but later returned to its station.

Occupation of a territory by a dominant fish in any population was difficult to define as the size of the territories were very large relative to the size of the channel. In Channel 1 especially the dominant fish frequently appeared to be patrolling the entire channel in a regular fashion, attacking subordinates as they were encountered. In Channel 2, the size of territories varied considerably, as did location of the territory holders' stations. Sometimes, with low populations, the same situation as in Channel 1 occurred in that the dominant patrolled the whole of the channel. On a few occasions much smaller territories were defended, usually at high population levels. In one instance (run 3) a fish successfully defended an area approximately 15 x 8 cm for two days. Intruding fish were attacked only when they came within 10 cm of the occupant, stationed in a narrow cleft between two large stones. At other times, territories approximately one third the size of the channel were defended but these did not appear to be well established and the defending fish often pursued an intruder far outside its usual territorial bounds and failed to return to its original station.

There was a considerable difference in the distribution and behaviour of the fish in the two channels when they were observed at times of more than two hours after feeding. In Channel 1 the subordinate fish were usually found in a fairly tight group in the downstream half of the channel, in the surface few centimetres of water, often with their dorsal fins breaking the surface. The dominant fish in Channel 1 swam deeper than the
subordinates and maintained almost constant levels of activity and aggression, irrespective of the time since the last feeding.

The fish in Channel 2 appeared to undergo a cycle of activity and aggression which was closely associated with feeding. Immediately after feeding (during the aggression monitoring) the distribution and behaviour of the fish did not differ greatly from that described for Channel 1, with the dominants generally swimming deeper than the subordinates and showing high aggression levels. As time after feeding increased, this distribution gradually became inverted so that at about 2-4 hours after feeding the subordinates were below the dominant, which swam at about midwater, and usually lay motionless between or behind stones. Subordinates did not remain grouped but were distributed throughout the channel wherever suitable resting-places were available. Low subordinate activity was accompanied by a much reduced (of Channel 1) dominant activity and aggression.

For Channel 2 it is impossible to say with any confidence whether the reduced activity of the subordinates caused the reduced dominant activity or vice versa. However, the difference in behaviour between the two channels suggests that mutual dominant/subordinate visibility was an important factor. In Channel 1 the subordinates were always visible to the dominant (and vice versa) and the typically dark colouring of the subordinates and their tendency to bunch made them conspicuous in the pale grey channel. The presence of these highly conspicuous subordinates appeared to provoke the dominant to continual high levels of aggression.

In Channel 2 the high levels of subordinate activity caused by feeding gave rise to a similar situation to that in Channel 1. After feeding, however, the subordinates were able to avoid the dominant by concealment in the substrate.

There was a noticeable difference in the colouring of the subordinates in
the two channels. Whilst Channel 1 subordinates were typically uniformly very dark, almost black in many cases with no contrasting spots or bars, the Channel 2 subordinates were dark with irregular light bars; this was an extremely effective camouflage in this environment of light and dark gravel particles. Colouring of dominants was similar in both channels, the fish being pale with the dark spots on the back, shoulders, and flanks appearing very small and only slightly contrasting.

2.3.3 Discussion The results from the second experiment confirm the inference drawn from the first that a physically complex environment will support a larger resident population of juvenile brown trout than a simple environment. In both experiments the complex environment was represented by simulated stream conditions in Channel 2. As in the behaviour experiments, significantly higher levels of aggression were observed in the simple environment, and were associated with the lower numbers of resident fish.

Territoriality was exhibited by fish in both complex and simple environments but territory size tended to be smaller in Channel 2, the complex environment, an observation similar to those of Kalleberg (1958) and Yamagishi (1962).

The association between low aggression and high carrying capacity in a complex environment and vice versa in a simple environment prompts the conclusion that simple environments have fewer residents because of the high levels of aggression. Chapman (1962) suggested a link between aggression and emigration for fry of coho salmon. The coho fry were found to emigrate mainly at night (70-98%) but, as Stringer and Hoar (1955) demonstrated that aggression decreased with decreasing light intensity, the case for aggressive behaviour being the immediate cause of emigration is weakened.
In the present experiment no distinction was made between day and night emigrants, so no conclusions can be drawn concerning this apparent paradox.

2.4
Third Carrying Capacity Experiment

2.4.1
Materials and Methods   The third experiment was designed to examine the correlation between aggression and carrying capacity apparent from the preliminary and second experiments.

Procedure was determined by the equipment which was available; the large tanks from BE3 and the divided tank from the previous carrying capacity experiments. Modifications were made to the two sets of tanks to make them similar with respect to depth, flow rate and photoperiod. The only major difference between the two sets of equipment was the light intensity, which could not be altered. A comparison of the two sets of equipment is given in Table 2.4.

As the fish used in this experiment were small, groups of 30 fish were used. An unexpected advantage of the small fish was their total lack of concern when they were transferred from one set of tanks to the other.

There were eight runs in the experiment, each following the same procedure. Environmental complexity was provided by the structures used in BE3, with two runs for each of the four structure types.

Each run was made up of three stages. In stages 1 and 2 the aggressive behaviour of the fish was monitored in the tanks from BE3. In stage 3 the performance of the fish in the carrying capacity tanks was studied.

The procedure for a typical run was as follows. The day before the run
### TABLE 2.4

A comparison of the two sets of tanks used in the third carrying capacity experiment.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>BF3 Tanks</th>
<th>Carrying Capacity Tanks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (excluding traps and screens)</td>
<td>220cm</td>
<td>200cm</td>
</tr>
<tr>
<td>Width</td>
<td>59.5cm</td>
<td>45cm</td>
</tr>
<tr>
<td>Mean depth*</td>
<td>12.75cm</td>
<td>13.5cm</td>
</tr>
<tr>
<td>Volume Flow</td>
<td>19.6 litres min⁻¹</td>
<td>13 litres min⁻¹</td>
</tr>
<tr>
<td>Linear Flow</td>
<td>24cm min⁻¹</td>
<td>20cm min⁻¹</td>
</tr>
</tbody>
</table>

**Light Intensity**

- At centre of tanks: 55-60 Lux to 600 Lux
- At ends of tanks: 45-50 Lux to 220 Lux
- In shadow of frame: -10 Lux
- In observation chamber: 5 Lux
- Inside tunnels: 5 Lux
- Immediately under banks: 5 Lux
- Halfway between banks and bottom of tank: 10 Lux to 15-20 Lux

*Mean depths are approximate values because actual depths varied due to distortion of the floors of the tanks.*
was to start a group of 30 fish was introduced to each of the BE3 tanks. Stage 1 lasted for two and a half days and there were no structures in either tank. On the first and second days the fish were observed once in the morning and once in the afternoon but on the third day they were observed in the morning only. A single observation consisted of 10 minutes aggression-monitoring before and after a 5-minute feeding period. In the afternoon of the third day both tanks were cleaned and one was chosen, by the toss of a coin, as the experimental tank.

Stage 2 was a repeat of stage 1, with five observations on each group of fish, but with the required set of structures added to the experimental tank. The control tank contained no structures in stage 2.

After the fifth observation of stage 2 the two groups of fish were transferred to the carrying capacity tanks. The group from the control tank was transferred to a channel containing no structures. The fish from the experimental tank were transferred to a channel with the same type, number and distribution of structures as in stage 2.

Stage 3 lasted for five whole days. Emigrant fish were removed and measured at the beginning and end of the photoperiod. Direction of emigration was recorded. At the end of stage 3, any resident fish were removed and measured.

Data was gathered on the effect of temperature upon aggressive behaviour and the relative frequency of aggressive interactions between fish of similar and different size.

2.4.2

Results 1) BE3 Tanks – Aggression/Structures The results from this part of the experiment were very similar to those of BE3. Aggression data for the four different structure types are shown in Figs. 2.3 - 2.6. Statistical analyses of the data showed that the tunnels, planks and banks had levels of aggression which were significantly lower, \( P = 5.0\% \) than
Fig 2:3 Aggressive behaviour of juvenile brown trout with changing environmental complexity
Stage 1. No structures in either tank
Stage 2. No structures in control tank; 6 tunnels in experimental tank
○○ Control tank ○○ Experimental tank
Fig 2.4 Aggressive behaviour of juvenile brown trout with changing environmental complexity

Stage 1 No structures in either tank
Stage 2 No structures in control tank; 6 blocks in experimental tank

- - Control tank  - - Experimental tank
Fig 2.5  Aggressive behaviour of juvenile brown trout with changing environmental complexity
Stage 1  No structures in either tank
Stage 2  No structures in control tank; 6 Planks in experimental tank
○-○ Control tank  ●-● Experimental tank
Fig 2-6  Aggressive behaviour of juvenile brown trout with changing environmental complexity
Stage 1  No structures in either tank
Stage 2  No structures in control tank; 2 Banks in experimental tank
○-○ Control tank  ○--○ Experimental tank
their controls, but that the levels of aggression recorded for groups of fish with blocks were not significantly different from those of their controls.

When a mean control was calculated, and the results from the four structure types made comparable by expressing aggression for any particular observation period as a percentage of the total number of aggressive acts for all observation periods for that group of fish, the structures could be ranked in order of 'effectiveness' in reducing aggression during stage 2, by using a Two-Factor Anovar. This ranking is shown in Fig. 2.7.

Throughout the experiment, comprehensive records were kept of the fish's reactions to the structures and of the behaviour of the control groups of fish.

In the control groups of fish, behaviour during stages 1 and 2 varied little from group to group. Distribution of the fish within the control tanks was affected by feeding but this effect was similar in all groups used, and was predictable.

In the pre-feeding observation it was rare to see the fish evenly distributed, either along the length of the tank, or through the depth of the water. On most occasions the fish were distributed according to one of two patterns. The first of these was termed the '2-groups distribution' and was characterised by the fish forming two loosely-knit groups, one in the upstream third of the tank and one in the downstream third, with very few fish in the central third. Of the two groups, the upstream one was usually the larger and most of its members swam above the bottom of the tank, from midwater to the surface. The downstream group were often seen lying on the bottom or swimming very close to it. The levels of activity and aggression in both up- and downstream groups varied considerably and one group was not consistently more active or aggressive than the other.
Fig 2.7 Diagramatic representation of the statistical comparison of the effects of the four structure types upon aggression in stage 2 of the third carrying capacity experiment. Figures are % levels of significance. NSD = No significant difference. Structure types ranked L to R in order of decreasing effect upon aggression.
The second commonly observed distribution was seen slightly more frequently than the '2-groups distribution'. It was recognised when all of the fish were in the upstream half of the tank. Even in this more 'condensed' distribution it was sometimes noticeable that the fish located at the upstream end of the group tended to swim or maintain position higher in the water than those at the downstream edge of the group. As in the '2-groups distribution' levels of aggression and activity varied considerably.

Before being fed, individual fish often maintained positions for several minutes. The positions so maintained did not have any common feature. There was no preference for shaded areas nor positions at any particular depth. Although fish did maintain position in this way and were involved in aggression from these positions, no interpretation as territorial behaviour is permissible as the aggression was not in defence of the position held nor did the position-holder return to its position after the aggressive interaction.

During other pre-feeding observations, position maintenance was seen infrequently and the level of activity was much higher. In these instances the activity was divided between aggressive behaviour and what was termed 'food-searching behaviour'. Fish showing food-searching behaviour swam either close to the surface or close to the bottom of the tank, moving forwards in a deliberate way, pausing frequently to inspect tiny particles of detritus or dust that were floating or lying on the bottom. When food searching on the bottom, many of the particles were taken into the mouth and quickly ejected but this 'tasting' process was seen only rarely at the surface.

When the fish were fed, the introduction of food was the beginning of a consistent sequence of events. Whichever way the fish were distributed when introduction of food began, only a few fish, perhaps seven or eight, were situated close to where the food entered the water.
As food was introduced the fish in the immediate area began to feed, initially taking sinking pellets, then rising to feed from the surface. Food pellets not eaten by these fish drifted down the tank in the flow and passed over other fish which rose, sometimes from the bottom, to take the pellets, when the more distant fish began to feed they swam up the 'food gradient' to the source of food. Consequently there was an aggregation of fish in the immediate feeding area. The sight of other fish feeding may have been another factor leading to aggregation but the main cause appeared to be individual fish following the stream of food to its source.

The time taken for the formation of the feeding aggregation varied, being especially long if the fish were slow to begin feeding, which meant that the food pellets became widely dispersed over the water surface and the food 'trail' was disrupted. As the fish became accustomed to the feeding procedure, the aggregations formed more quickly. This may have been an indication of the fish learning the location of the food source.

Within the feeding aggregations the fish showed a strong preference for feeding at the surface, largely ignoring the food pellets which sank, but in each group there were a few individuals that fed off the bottom and as a result enjoyed a temporary abundance of food whilst the other fish in the group were feeding on the floating pellets.

When food was no longer being introduced, the amount available to the aggregated fish rapidly declined and, as it did so, fish began to drop down to the floor of the tank to pick up the sunken pellets. The 'dropping down' was the beginning of the disposal of the aggregation, which continued with the fish searching an increasing area for remaining food. Dispersal usually took between five to eight minutes and was complete when the fish were once again in a typically pre-feeding distribution.

The feeding aggregation was a prominent feature of every group's behaviour.
An integral part of the aggregation was that played by aggressive behaviour. As well as being the cause of aggregation, feeding also influenced aggression, which was in turn involved with aggregation formation and dispersal.

In common with other experiments and much published data, feeding in this experiment had the effects of firstly, greatly reducing or eliminating aggressive behaviour during feeding, and secondly of causing higher levels of aggression after feeding than before. The initial effect of feeding, that of largely eliminating aggression in the groups of fish may have 'allowed' the feeding aggregation to form, because, with its active fish and high number of fish to fish contacts, the aggregation created a situation with a potentially very high level of aggression. The aggregation could only continue as long as aggressive behaviour was suppressed by the availability of food.

As soon as the introduction of food ceased, aggression immediately became apparent and as the amount of available food decreased, the level of aggression rose until it reached the potential which existed in the aggregation. Consequently, the dispersal of the aggregation, which began by fish searching for remaining food was accelerated by the sudden increase in aggressive behaviour, resulting in total dispersion of the aggregation. During the process of dispersal the level of aggression declined and eventually reached its pre-feeding level.

In half of the control groups of fish the phenomenon of escape swimming was observed. Only one or two fish exhibited this behaviour in each group, and those fish were always at the upstream end of the tank. Escape swimming was usually only seen during the first one or two observations and most often stopped after the fish had been fed for the first time.

The behaviour of the groups of fish in the experimental tanks was essentially the same as in the control tanks in stage 1, when there was
no difference between the control and experimental tanks. In stage 2, the presence of the structures influenced behaviour to varying degrees, depending upon the structure type. Two structure types stimulated some territorial behaviour and the others influenced distribution and the feeding aggregation.

1) Tunnels The presence of tunnels in the tanks did not greatly alter the distribution of the fish, sometimes the group of fish was located below the level of the tunnels and, on other occasions, above it. Feeding aggregations in the experimental groups formed in the same way as in control groups, with a majority of surface-feeding individuals.

In both runs using tunnels fish showed repeated temporary associations with the structures, lying just downstream of, or inside the structures. Another frequent observation was of fish swimming through the tunnels.

Territorial behaviour was seen five times in one of the two runs. The areas which were defended all included a tunnel but the territory-holding fish did not always choose the inside of the tunnel as the 'focal point' of the territory, sometimes remaining just downstream of the opening. The territories were maintained for short periods only and were usually vacated during feeding, the territory-holder not returning after feeding.

One piece of unusual behaviour was shown by a territory-holding fish when it threatened a larger intruder which retaliated by nipping. When this happened the territory-holder reacted by turning and rapidly entering the tunnel. This was the only instance of a fish using a structure as shelter from the aggression of another fish that has been recorded during the entire investigation.

When, at the end of stage 2, the fish were disturbed by the process of transferring them to the carrying capacity tanks, the tunnels were used extensively as fright cover. As many as 14 fish used the same structure and hiding fish remained inside the tunnels until several minutes after
the disturbance had ceased.

2) **Blocks**  Blocks had no noticeable effect upon either the distribution of the fish or feeding aggregations.

The fish showed very little association with the blocks although occasionally individual fish would align themselves with the end or one of the long edges of the blocks. The most common form of behaviour concerning the blocks was a close 'inspection' of the surfaces of the structures, in a manner similar to the food searching behaviour described above.

One fish established a territory when blocks were present. This particular territory was held for the longest period of any of those seen in this experiment, being first seen in the afternoon observation of one day and persisting until the following morning. The focal point of this territory was not associated with any of the blocks but appeared to be at a point immediately beneath the feeding mechanism. The size of the territory was bounded by three of the blocks. The territory-holder was one of the smaller fish of the group and made repeated, successful defences of its position against larger intruders. Defence of the territory was weakest during feeding and strongest in the post-feeding observations.

The location of the focal point of the territory, away from any of the structures, suggested that this may have been an instance of food-linked territoriality, with the territory-holding fish gaining a feeding advantage.

When disturbed, the groups of fish made no use of the blocks as fright cover, showing instead the typical reaction of control groups of fish, and forming fright huddles in corners of the tank.

3) **Planks**  No instances of fish establishing territories were seen when planks were the structures in the experimental tanks. Very little
association of any kind between the fish and planks was seen, although sometimes fish would temporarily take up a position in the angle formed by the plank and one of its supports. As with the blocks fish would closely inspect the surfaces of planks, frequently nibbling at their flat surfaces.

In both runs the presence of the planks affected the distribution of the fish and the feeding aggregations. Distribution of the fish changed during stage 2 in that the fish became more localised and remained in the upstream half of the tank for most of the time. This change took place slowly at first but was most noticeable after the third observation.

Feeding aggregations were, especially early in stage 2, slower to form in tanks containing planks than in control tanks. The most likely cause of this effect was the visual interference caused by the planks. As well as being slow to form, the aggregations were also slow in dispersing, and this may have been caused by a 'containing effect' of the planks on the food pellets, hampering their dispersal.

Planks were not used as fright cover when the groups of fish were subjected to overhead disturbance. Individual fish did try to shelter in the angles of the planks and their supports but were unable to do so and soon left these positions to join the fright-huddles.

4) Banks. The presence of the banks in the experimental tanks did not stimulate any territorial behaviour. The fish showed a slight tendency to avoid the areas of shade created by the banks, and consequently the distribution of the fish was affected.

In a similar way to that seen in the case of the planks, the fish in the tanks with banks appeared to be 'contained' by the structures. Fig. 2.8 shows the typical distribution in the experimental tanks, with the majority of the fish in a loose shoal in the upstream half of the tank, and scattered individuals elsewhere.
Fig 2.8 Distribution of the group of fish in the experimental tank with banks as the structures providing environmental complexity.

B Banks
F Feeding apparatus
U Upstream end of tank
Feeding aggregations formed normally when banks were present but were slow to disperse and this may have had a similar cause to that suggested for the planks.

Although there was a general avoidance of the banks, individual fish occasionally stayed underneath them for short periods, usually lying close to the surface and often showing the inspection/food searching behaviour seen with other structures. Fish which did maintain positions under the banks showed no attachment to their positions and were easily displaced from them.

The banks were used as fright cover when the groups of fish were disturbed. The response to disturbance was not as complete as was seen in the case of the tunnels, however, as small fright-huddles did form initially in the corners of the tanks. If the disturbance continued these huddles broke up, the fish settling under one or other of the banks. As in the previous experiment (BC3) the fish sheltering under the banks always lay on the bottom of the tanks, in contrast to the surface position of fish merely resting under them. The duration of hiding under the banks was short compared to the tunnels, as fish would leave the shelter of the banks immediately after the disturbance ended.

2) BC3 Tanks - Additional data on Aggression  a. Behavioural Repertoires

Although the fish used in this experiment were, at the beginning of the experiment, only two months old, and had lived exclusively in a hatchery trough, they possessed a complete repertoire of aggressive behavioural patterns. All of the threat, defensive and submissive postures seen with larger fish were present in the behaviour of the small fish.

There were, however, differences between the aggressive behaviour of the larger and smaller fish. In the smaller fish, the displays tended to last much longer and were often performed for between five and seven seconds. Another difference was that, in small fish, the wigwag display
was seen much less frequently than in groups of larger fish. This may be an indication of an absence of a social hierarchy in the groups of small fish.

The aggression of the small fish was also different from that of larger fish in that the lateral threat was used much more often as a defensive display in the former. A final difference was that, in small-fish groups, there was no 'persecution' of one fish by another. The dominant individual of a group of large fish frequently repeatedly attacked the same subordinate, usually in preference to other, nearer subordinates, but this type of behaviour was not seen in small fish. One reason for this may have been the higher number of fish in the groups which could have prevented individual recognition by the fish.

Aggressive interactions between fish in this experiment almost invariably resulted from one fish approaching another. The initiator of the interaction was usually the fish which was approached. This was especially noticeable when fish maintaining positions were approached by mobile fish. This type of aggressive behaviour might have been expected to produce a distribution of fish with stable inter-individual distances, which could be regarded as a precursor of a territorial mosaic, but such distributions were not observed.

b. Aggression and Temperature. In each of the last five runs of this experiment, the water temperature was recorded at each observation. For the period when temperature records were kept, the mean temperature was 15.95°C (n = 49, S.D = 1.20°C). Maximum temperature recorded was 18.4°C, and minimum 13.4°C. During any one run, temperature range was between 1.4 and 3.8°C. Statistical analyses of these data did not reveal any significant correlation between temperature and frequency of aggressive acts in either the control or experimental groups of fish. It is thus unlikely that any of the variation in aggression between groups of fish resulted from temperature differences.
c. Aggression and Size. Because it was noticeable that smaller fish of the group readily attacked larger individuals, the number of aggressive interactions initiated by fish which were obviously smaller than the other contestant were recorded separately for runs 3-8.

There was no statistically significant difference between the proportions of small-initiated aggressive acts in control and experimental groups of fish. Neither was there any significant correlation between time and the proportion of small-initiated aggressive acts.

Overall, the interactions initiated by smaller fish averaged about 19% of the total observed aggression. That this proportion is so high suggests that there was no size-based hierarchy operative in these groups of fish.

d. Feeding and Aggression. The effect of feeding upon aggression and the relationship between time and this effect was very similar to that seen in BE3. Fig. 2.9 shows how the effect of feeding declined with time from the start of the experiment. There was an inverse correlation between time and effect of feeding, significant at \( P = 1.0\% \). There was no significant difference in the effect of feeding upon aggression between experimental and control tanks.

3) Carrying Capacity Tanks - Carrying Capacity/Structures. The basic data obtained during stage 3 were the numbers and sizes of emigrants and residents in control and experimental channels. Direction of emigration was also recorded.

The numbers of residents in the control and experimental channels were compared, using a Two-Factor Anovar, which indicated that for tunnels, planks and banks there were significantly \( (P = 0.1\%) \) fewer residents in the control channels. For blocks the control channels had fewer residents but the difference was significant at \( P = 5.0\% \). Fig. 2.10 shows the comparison between experimental and control resident populations.
Fig 2.9 The effect of feeding on aggression in the third carrying capacity experiment. Mean of all runs (See text for calculation)
Exponential curves of the form $Y = b e^{mx}$ where $Y =$ time (hours), $b =$ Y intercept, $m =$ slope and $x =$ number of residents can be fitted to the data presented in Fig. 2.10. Table 2.5 shows the slopes of the fitted curves. It can be seen for each control/experimental pair that the control channels have the higher values of $m$, that is to say higher rates of emigration, than the experimental channels.

If the data from each structure type are compared with each other and with a 'mean control', using a Two-Factor Anovar, the structure types can be ranked in order of the size of the resident populations. The ranking, in order of decreasing resident population size were Tunnels > Banks > Planks > Blocks > Mean controls.

As emigrants were removed from the traps at the beginning and end of the photoperiod, it was possible to compare the numbers of day and night-time emigrants. Because the dark period was longer than the light, it would have been expected that there would be more night-time than daytime emigrants. Using a $X^2$ test, it was possible to compare the expected and observed numbers of day and night-time emigrants. For the pooled control channels there were significantly more night-time emigrants than would be expected, at $P = 1.0\%$. For the experimental channels there were also more emigrants than would be expected at night, but in this case with $P = 5.0\%$.

This part of the data was further analysed by using a Single-Factor Anovar. It was found that during the day there was no significant difference between the numbers of up and downstream emigrants in either the control or experimental tanks. At night, however, there were significantly more downstream emigrants at $P = 0.1\%$ for control and $P = 1.0\%$ for experimental tanks.

It was also possible to compare the sizes of up and downstream emigrants, and residents. A Single-Factor Anovar was used in this analysis. The
Fig 2·10 Resident population sizes in control and experimental channels during stage 3 of the third carrying capacity experiment. Structure type as headings. ▲▲▲ Control channel ▲▲▲ Experimental channel
TABLE 2.5

<table>
<thead>
<tr>
<th>Structure Type</th>
<th>Experimental</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tunnels</td>
<td>-0.0084</td>
<td>-0.0048</td>
</tr>
<tr>
<td>Blocks</td>
<td>-0.0224</td>
<td>-0.0098</td>
</tr>
<tr>
<td>Planks</td>
<td>-0.0116</td>
<td>-0.0100</td>
</tr>
<tr>
<td>Banks</td>
<td>-0.0136</td>
<td>-0.0096</td>
</tr>
</tbody>
</table>

Slopes (m) of the exponential curves fitted to the relationships between time and resident population size in stage 3 of the third carrying capacity experiment.
full comparison is shown in Fig. 2.11. Upstream emigrants tended to be larger than downstream emigrants. Residents were either the same size or smaller than upstream emigrants and the same size or larger than downstream emigrants.

The behaviour of the fish in the control tanks during stage 3 was essentially the same as that seen in the BE3 tanks, with loose 'subordinate shoals', either at the up or downstream end of the channel or a 'two-groups' distribution. The reason for the preference of the fish for the ends of the channel may have been the light intensity in the channels. As the light was situated at the centre of the channels there was an appreciable light gradient from the centre to the ends of the channels.

In experimental channels containing tunnels or banks the fish showed much more association with the structures in the carrying capacity channels. This was especially noticeable with the tunnels as most of the fish spent the majority of the time inside or very close to the structures, emerging to feed and then returning to their original position. Similarly, the fish with banks showed a much greater tendency to remain under them emerging to feed and then returning. Behaviour in channels containing blocks or planks was similar to that seen in the BE3 tanks. Fish were also more susceptible to disturbance in the carrying-capacity channels and would form fright huddles, or hide in the tunnels or banks, at the slightest provocation.

The most probably reason for the increased 'use' of the structures providing overhead cover was the higher light intensity in the channels as this made the areas of shade created by the structures contrast more with the rest of the tank than in the BE3 tanks.

4) Correlations Between data from Carrying-Capacity and BE3 tanks. A product-moment correlation coefficient was calculated to test for
Fig 2.11 Diagramatic representation of the statistical analysis of the size (length) of up- and downstream emigrants and residents in stage 3 of the third carrying capacity experiment. Figures are % levels of significance. NSD No significant difference. C Control channel, E Experimental channel, D Downstream emigrants, U Upstream emigrants, R Residents.
correlation between aggression and carrying capacity. To do this the aggression of each group of fish was expressed as the total number of aggressive acts recorded in stage 2, and performance in stage 3 was expressed as the number of fish-days obtained. This latter was calculated by summing the number of residents in the tanks at 24-hourly intervals during stage 3. There was a negative correlation between total stage 2 aggression and the number of fish-days obtained, significant at $P = 5.0\%$.

A linear regression may be fitted to the data, the equation for which is

$$Y = 70.625 - 0.0376 (x- 1488.44) - (3182.0487 + 0.001119 (x- 1488.44)^2).$$

This is shown in Fig. 2.12 from which it can be seen that the 95% confidence limits are very wide, and that there is considerable scatter in the actual data.

2.4.3 Discussion

The statistically significant correlation between the number of fish-days obtained in stage 3, and the total aggression in stage 2 suggests that the carrying capacity of the tanks was influenced by the complexity of the tanks, by means of the aggressive behaviour of the fish.

When the structures and mean control were ranked according to the size of the resident populations, the mean control was at the 'end' of the ranking, with the lowest resident population, and the structures were ranked in similar order when compared with the aggression rankings (Fig. 2.7), the tunnels having the lowest aggression and highest resident population. The only difference between the two rankings was that the positions of the planks and banks were reversed.

The reversal of position between the planks and banks was probably a consequence of the higher light intensity in the carrying capacity channels. In the 'brighter' carrying capacity channels it was noticeable that fish showed a much stronger association with the banks than in the
Fig 2.12 Relationship between aggression and resident population size in the third carrying capacity experiment, with the fitted line
BE3 tanks. This may have resulted in lower levels of aggression with banks than with planks in the carrying capacity channels.

If it were assumed that there was a correlation between aggression and carrying capacity, it would be expected that most of the emigration would occur during the day. However, analysis of the numbers of day and night emigrants showed that there were more night-time emigrants than was expected and suggested that the cause was the high numbers of downstream emigrants. This was so for both control and experimental tanks.

This information poses problems in the interpretation of the ways in which complexity influenced the numbers of emigrants. Two hypotheses are possible on the assumption that higher rates of downstream, night-time emigration were the cause of the different resident population sizes.

Firstly, it could be argued that, in spite of the statistical evidence supporting a connection between aggressive behaviour and carrying capacity, there was no real correlation. The two parameters may both have been affected by complexity of the environment but there need not have been a causal relationship. If this were so, the differences in the sizes of resident populations may have resulted from the effect of the structures on the physical processes of emigration.

It is known that, at night, salmonids in streams stay close to the substrate and are largely inactive during darkness (e.g. Hoar 1953). Position maintenance in these conditions must be possible as fish stay in the same location for relatively long periods. A likely method is one involving tactile stimulation from the environment. In the control channels fish may have received very little tactile stimulation from the environment and so may have been passively swept into the downstream trap. In the channels containing structures there were more tactile
stimuli available, to which the fish could orientate, avoiding such passive emigration.

The 'passive emigration hypothesis' has several faults. In the control channels it was possible that if the fish dropped to the bottom in darkness they could have been displaced downstream because of the lack of tactile stimuli. But, as the dams were passable only at the surface, such displacement would have been expected to result, not in emigration, but in an accumulation of fish above the downstream dam. Neither could passive emigration have accounted for the upstream, nighttime emigrants. Further evidence against this hypothesis comes from the fact that the structures with the highest resident populations were not those providing maximum tactile stimuli.

The second hypothesis is that fish emigrated actively from the channels. Fish emigrated because the environments provided by the channels were inadequate. The environments may have been unsuitable because of the lack of cover, or the aggression within the groups of fish. It is impossible to separate the effects of aggression and complexity in this respect but the combination of the two may be regarded as creating an 'emigration pressure' proportional to the unsuitability of the environment. Whilst this might account for the ranking of resident population size according to structure type and for the similarity between this ranking and that of aggression with the structure types it does not explain why there should have been more nighttime emigrants than expected.

If there was an 'emigration pressure' in the tanks, which was at least partly created by aggression, it would have been expected to be felt more acutely by the smaller, subordinate fish. Consequently these fish would have been expected to make up the bulk of the emigrations and this was indeed the case, as the downstream emigrants tended to be smaller than the residents and were probably subordinate to them.
During daylight the activity of the subordinate fish may have been inhibited by a reluctance to leave the security of the subordinate shoal or association with structures and by the high light intensity in the channels. Daytime emigration may have resulted from direct aggression, but as it was similar at all levels of complexity, aggression may not have been the main cause.

At night the inhibition of the subordinates was removed, as the level of aggression dropped, perhaps to zero. As the subordinates were no longer 'tied' to the security of the shoal, or structures, if present, they were able to migrate from the channels in an active manner. The higher number of downstream emigrants may have resulted from it being physically easier for the fish to emigrate downstream.

In conclusion, this experiment demonstrated that the carrying capacity of, and the level of aggression in an environment were both influenced in a similar way by the complexity of the environment. Whilst it is possible that complexity influenced carrying capacity because of its effect upon aggression, evidence for this was inconclusive.
3. EXPERIMENT ON THE EFFECT
OF ENVIRONMENTAL COMPLEXITY
UPON THE GROWTH OF
JUVENILE BROWN TROUT
Introduction

Many factors affect the growth of fish. Of obvious importance are quantity and quality of the food supply (e.g., Brown, 1951; Baldwin, 1956; Davis and Warren, 1970) and temperature (Brown, 1946 III, 1951 and McCormick et al., 1972).

Light is perhaps a less obvious factor than food or temperature but Bilton (1972), working with Sockeye salmon (Oncorhynchus nerka), Brown (1946 II) with brown trout and Pyle (1969) with three trout species, all demonstrated significant effects of light, especially photoperiod, upon growth.

Within a single population of fish, growth of individuals can be influenced by social organization of the population. Allen et al. (1948) showed that, in populations of green sunfish (Lepomis cyanellus), there was a correlation between social rank and growth rate, with alpha-fish (dominant) growing faster than lower ranking associates. Social rank also affected the feeding behaviour of sunfish, subordinates appearing unable to feed as freely as dominants.

Magnuson (1962) demonstrated that, for the medaka (Oryzias latipes), social dominance influenced growth only when food was limited and localised. For trout, growth dependence has been recorded under conditions where food was neither limited nor localised. Brown (1946 I, 1951) found that larger brown trout fry grew faster than smaller fry and later suggested that the smaller fish may have suffered some form of physiological stress because of their socially subordinate position, leading to their being unable to utilise as much of their food intake for growth as the dominant fish. Similar observations were made on rainbow trout by Yamagishi (1962).

If, in brown trout, the 'size-hierarchy effect' upon growth is mediated
by aggressive behaviour, then it might be expected that parameters affecting aggression would, in turn, influence growth. As it was known from other experiments in this investigation (BE1 - BE3) that environmental complexity profoundly influences aggressive behaviour, this experiment was performed to compare the growth of groups of trout held in environments of different complexity.

3.2
Materials and Methods

The apparatus used in this experiment is described in Section 2 of the Appendix. Two environment types were designed and are referred to as complex and simple. The channel representing the simple environment was left with the floor bare, whilst the other, provided with coarse gravel, large and small stones (3-10cm in size) and several clumps of aquatic moss, represented a complex environment. Depth of water was constant at 13.5cm in the simple environment but varied, according to the substrate, from 2.0 to 13.0cm in the complex environment. Water velocity varied according to depth in the complex environment but was steadier in the simple environment.

Each environment supported a population of 12 fish which, at the beginning of the experiment were of comparable size. After a two week 'settling-in' period, the fish were removed from the channels, anaesthetised in a 116000 solution of MS222 Sandoz, measured and weighed and returned to their respective channels. This first weighing was taken as Week 0 of the experiment, and the fish in each population were allocated ranks, from 1-12, in order of decreasing size. For the rest of the experiment it was assumed that each fish retained its original size rank position (Brown, 1946 I). Weighings were carried out at fortnightly intervals from Week 0. Weighings always took place on Monday mornings.

The fish were fed with a commercial, pelleted food, which was introduced to the channels by means of a glass tube approximately 1m long and 15mm
diameter. This was a convenient way of ensuring that the food was introduced slowly enough for most of the pellets to be eaten. Throughout the experiment, both populations were given a food ration of 10% biomass per week. This ration was fed to the fish over the five days from Monday to Friday which meant that at weighings the fish had not been fed for two days beforehand. There were two feeds per day at the beginning of the experiment, changing to four feeds per day when larger quantities of food were involved. The two channels were always fed at the same times and the same number of times per day. New ration weights were calculated after each weighing and were used for the following fortnight.

The experiment ran for 20 weeks.

3.3 Results

Table 3.1 shows the specific growth rates (SGR) (Brown, 1946 I) for each fish in both populations, calculated from the formula:

\[
\text{SGR} = \frac{\log_{10} \frac{W_{t2}}{W_{t1}}}{t_2 - t_1} \times 100\%,\quad \text{where} \quad \text{SGR} = \text{specific growth rate}, \quad W_{t2} = \text{weight at time } t_2, \quad W_{t1} = \text{weight at time } t_1, \quad \text{where } t_2 \text{ is later than } t_1. \]

With time measured in weeks, SGR is expressed as percent weight per week.

Analysis of the data in Table 3.1 by means of a Two-Factor Anova (size rank and environment type) showed that there was no significant difference in SGR's between populations.

Correlation coefficients were calculated for both environments to test for association between size rank position and growth rate. In the simple environment there was a significant positive correlation \((P = 0.1\%)\) for fish ranked 2-9, with \(r = 0.9441\). In the complex environment there was a negative correlation for the whole population significant at \(P = 0.1\%\), with \(r = 0.9486\). Fig. 3.1 shows the two populations' size rank position/SGR relationships.
Specific growth rates of two populations of juvenile brown trout kept in environments of different complexity. Individual fish ranked in order of decreasing initial size. Food ration 10% biomass per week; experimental period 20 weeks.

<table>
<thead>
<tr>
<th>Size Rank Position</th>
<th>Simple-environment population</th>
<th>Complex-environment population</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8.545</td>
<td>9.417</td>
</tr>
<tr>
<td>2</td>
<td>7.878</td>
<td>9.007</td>
</tr>
<tr>
<td>3</td>
<td>8.036</td>
<td>8.993</td>
</tr>
<tr>
<td>4</td>
<td>7.855</td>
<td>8.970</td>
</tr>
<tr>
<td>5</td>
<td>8.160</td>
<td>8.713</td>
</tr>
<tr>
<td>6</td>
<td>8.269</td>
<td>8.354</td>
</tr>
<tr>
<td>7</td>
<td>8.517</td>
<td>8.669</td>
</tr>
<tr>
<td>8</td>
<td>Died week ten</td>
<td>7.806</td>
</tr>
<tr>
<td>9</td>
<td>8.699</td>
<td>6.817</td>
</tr>
<tr>
<td>10</td>
<td>7.955</td>
<td>6.423</td>
</tr>
<tr>
<td>11</td>
<td>Died week ten</td>
<td>Died week thirteen</td>
</tr>
<tr>
<td>12</td>
<td>4.867</td>
<td>6.730</td>
</tr>
</tbody>
</table>
Fig 3.1 Relationship between SGR and size rank position for 2 populations of juvenile brown trout kept in environments of different complexity
Food ration 10% biomass per week
Experimental period 20 weeks
○--○ Simple environment  ○—○ Complex environment
Lines fitted by linear regression (Ranks 2–9 only in simple environment)
Statistical comparisons of SGR were made between environments for the five largest surviving fish (ranks 1-5) and the five smallest (ranks 6, 7, 9, 10 and 12) in each population. For the large fish, those in the complex environment had significantly (P < 0.1%) higher growth rates than those in the simple environment. There was no significant difference between environment types for the small fish.

Food conversion efficiencies were calculated from: \( E = \frac{B_f - B_i}{C} \times 100\% \), where \( E \) = conversion efficiency, \( B_f \) = final biomass, \( B_i \) = initial biomass and \( C \) = consumption of food, with \( B_f, B_i \) and \( C \) measured in the same units. Dry weights of fish and food were used, obtained by drying samples of food and fish at 105°C for 24 hours and using the ratio between wet and dry weights to calculate dry weights of food rations and live fish. Conversion efficiencies were slightly higher in the complex environment at 22.4%, compared with 20.9% in the simple environment.

Aggressive behaviour was observed in both populations. There was more frequent and more persistent aggression in the simple environment, but no quantitative measurements of aggression were made in this experiment.

Distribution of the fish differed with environment type, except during and immediately after feeding, when the fish were concentrated in the immediate feeding area. In the simple environment the fish were almost invariably found in a loose shoal at the 'downstream end' of the channel, with the largest, apparently dominant fish at the head of the shoal. In the complex environment the fish were much more evenly distributed throughout the available space and took advantage of the cover afforded by the stones and clumps of moss. Similar distributions were seen in the second carrying capacity experiment (Section 2.3).

The clumps of moss were used as fright cover if the fish were disturbed.

During feeding, the dominant fish in both populations appeared to take a disproportionately large amount of food. With the exception of the
smallest fish in each population, which frequently did not feed at all, subordinates' feeding behaviour was influenced by environment type.

In the complex environment the fish showed a distinct preference for floating or slowly sinking flood pellets and seemed reluctant to take food from the bottom. Fish in the simple environment showed no such preference and took as much food from the bottom as from the surface.

It seems likely that the nature of the substrate may have been responsible for the observed differences in feeding behaviour, as the food pellets were much more conspicuous on the floor of the simple environment than in the gravel of the complex channel. As a consequence, food was available throughout a greater volume of water in the simple environment.

Dominant fish in both environments monopolised the point of entry of the food, apparently by virtue of their greater size, as aggressive behaviour was never observed during feeding. In the complex environment, subordinates obtained an amount of food in proportion to the length of time that they were able to remain in the immediate feeding area. This appeared to be governed by physical strength alone and smaller subordinates obtained relatively less food than larger ones. Because of their predilection for floating pellets, the complex environment subordinates did not take advantage of those pellets which sank beneath the dominant fish.

Subordinates in the simple environment were not 'preoccupied' with floating pellets and were seen to swim beneath the dominant and largest subordinates, picking up food from the bottom of the channel. Consequently, all but the smallest subordinates appeared to consume relatively equal amounts of food in the simple environment.

At the end of the experiment there were differences between environments in the physical condition of the fish. Practically all of the fish in the complex environment were fully-scaled and had perfect fins. The only fish in similar condition in the simple environment was the dominant
individual, all of the subordinates suffering, to a greater or lesser extent, split and frayed fins and loss of scales, usually from the shoulder. This deterioration of the simple environment subordinates may have been caused directly by aggression (see Section 1.2.3) or possibly by a lowered resistance to disease; this was not clarified.

3.4

Discussion

Whilst there were differences in the growth rates of trout between the two environment types and aggression was, as expected, much more frequent in the simple environment, interpretation of the data from this experiment is complicated by the effect of environmental complexity upon the feeding behaviour of the fish.

In the complex environment it is probable that the dominant fish obtained a disproportionately large amount of food and that the subordinates obtained relatively less food with decreasing size. This differential in food consumption was reflected in the relationship between size rank position and individual SGR. That this relationship was linear could be taken to suggest that there was a linear hierarchy in this population but observations of aggressive behaviour were too infrequent to substantiate or deny this suggestion.

Different results might have been obtained if food had been introduced over a wide area instead of being localised, avoiding the situation where the amount of food obtained by individual fish in the complex environment was governed by their ability to resist physical displacement from the immediate feeding area.

In the simple environment subordinate fish appeared to consume amounts of food proportional to their size, with the exception of the two smallest fish which ate much less and consequently exhibited lower growth.
rates than the rest of the population. However, the apparently
equivalent food consumption of ranks 2-9 did not result in these fish
showing similar growth rates. Observations of aggressive behaviour in
the simple environment indicated that the dominant fish alone was
responsible for the majority of the aggressive behaviour and that it
directed most of its aggression towards the larger subordinate fish.
Similar 'victimisation' of larger subordinates was observed in the
behavioural experiments presented earlier, and occurs, presumably,
because the larger subordinates present more of a threat to the social
position of the dominant than do the smaller subordinates (see also

The observation that, in the simple environment, smaller subordinates
grew faster than larger may have resulted from the larger subordinates
suffering considerably more aggression from the dominant and
consequently being more active and, perhaps, under more 'stress'
(Brown, 1957).

The significantly faster growth of the fish in size-rank positions 1-5
in the complex environment than equivalent-ranked fish in the simple
environment may also be a result of the higher levels of aggression in
the simple environment. High activity, associated with the high
aggression (BE1) may have meant that, in the simple environment, a
smaller proportion of the food consumed was available for growth. The
slightly lower food conversion efficiency recorded for the simple
environment supports this suggestion.
4. SYNTHESIS
The results of this investigation demonstrated that environmental complexity is an extremely important factor in the life of juvenile brown trout. An intricate network of interrelationships was found to exist among individual growth rates, population size and aggressive behaviour with all of these parameters influenced, directly or indirectly, by the complexity of the environment. To attempt a description of the network of interactions would result in confusion but the essential elements are summarised clearly in a 'flow-diagram', Fig. 4.1.

It must be emphasised that the information presented in Fig. 4.1 was derived from data obtained in the laboratory and consequently should not be interpreted as a representation of a 'natural' sequence of events. Caution is essential when applying the results of laboratory studies to populations of wild animals but it is possible to draw certain parallels between the findings of this investigation and published ecological work, especially in the field of population regulation. There are close similarities between Fig. 4.1 and parts of the diagram presented by McFadden (1969), summarising population-limiting mechanisms for stream-dwelling salmonids.

For juvenile brown trout in particular, population regulation is widely recognised as a behavioural mechanism, with territorial behaviour playing a large part. Soon after emergence from the redd, populations of brown trout fry establish territorial mosaics (e.g. Kalleberg, 1958; Heland 1971(b); Le Cren, 1972a) which result in downstream displacement of non-territory-holding individuals. Initial density of fry does not affect the number of fish able to obtain territories (Heland 1971(a)) unless it is below the potential 'carrying capacity' of the environment (Le Cren 1960, 1961 and 1965). A factor which does influence the number of territories available to fry is the complexity of the environment; Stuart (1953) and Kalleberg (1958). Increase in complexity was found to be associated with decrease in average territory size and
Fig 4.1 Summary of interactions among environmental complexity, aggressive behaviour, growth rate and population size for juvenile brown trout.
Parameters in heavy blocks were the main subjects of investigation.
Thickness of linking arrows indicates intensity of influence.
hence an increase in population density.

The length of time for which territorial mosaics exist is short, as the conditions which must be satisfied in order to allow a mosaic to persist are stringent. These conditions are that there must be: uniformity of substrate; uniformity of fish size; uniformity of 'aggressiveness' of fish; lack of position change (Jenkins, 1969). As fry grow, mosaics become disrupted. Larger fish are less intensely territorial and prefer to defend 'lisa' or positions (Le Cron 1972).

ERRATUM
Page 152  Le Cron (1972)
should read Le Cron (1972b)

mechanism by which territories are maintained. If the size of a population of trout fry is governed by territorial behaviour then the population is governed by aggression. And if there are smaller territories in a more complex environment then complexity reduces aggression, which was the basic conclusion of the present study. The significant inverse correlation found between levels of aggression and population size also agrees with published data on population regulation although in the present experiments aggressive behaviour was not associated with territorial mosaics.

Results of experiments concerned primarily with aggressive behaviour were largely compatible with published work. Relationships between
aggression and fish density were similar to those reported by Keenleyside and Yamamoto (1962) for juvenile Atlantic salmon. Feeding has generally been reported to cause a short-term increase in the amount of aggressive behaviour exhibited by groups of fish (e.g. Newman 1956) but in this investigation the effect of feeding upon aggressive behaviour was found to diminish exponentially with time from the beginning of the experiment. This observation supports the statement by Jenkins (1969) that "the importance of the time factor cannot be overemphasised in studies of trout social structures....".

One major divergence between present and published findings was in that section of the work concerned with the effects of different types of structure upon the aggressive behaviour of juvenile brown trout. The results of BE3 were diametrically opposed to those of Hartman (1963) who concluded that structure type had no significant effect upon the amount or nature of aggressive behaviour. The evidence available in the literature relevant to the effects of complexity upon density, distribution and territoriality would seem to dispute Hartman's suggestions, at the same time lending support, albeit indirectly, to the conclusions of this investigation.

The higher growth rates of trout kept in a complex environment may be of relevance to those concerned with the culture of fish but any practical application of these findings is unlikely for two main reasons. First, and most important, is the unnaturally high densities of fish used in modern cultural techniques. Environmental complexity influenced growth because of its effect upon the aggressive behaviour and social structure of the groups of fish used. Social structure is dependent upon fish being able to recognise other group-members individually (e.g. Jenkins 1969). Such a situation would never arise in a modern
hatchery trough or tank because of the number of fish present. Second, an almost universal hatchery practice is size-grading of fish at short time intervals, which would destroy any size-based hierarchies even if they did become established. Grading is widely believed to promote faster growth of the smaller fish but Pyle (1966) was able to find no significant difference in growth between graded and ungraded lots of hatchery fish and suggested that the main advantage of grading was one of commercial convenience.

Although the effects of complexity as examined in the present study are inapplicable to modern fish-cultural techniques, it is not true to suggest that the design (equivalent to complexity) of fish-holding facilities exerts no influence upon the quality of the fish produced. Fortney (1939) described 'naturalistic raceways' which incorporated dams, riffles and pools and claimed that healthy and vigorous fish were produced with negligible mortality. Design of rearing ponds can also influence the survival of hatchery fish after they are stocked. Burrows and Chenoweth (1970) designed a sophisticated rearing pond which produced fish with improved post-stocking survival. Rectangular recirculating ponds operated an enforced process of natural selection producing tougher and more resilient fish which were better able to withstand the rigours of stream life than the normal 'soft' hatchery fish (see also Miller, 1958 and Vincent, 1960).

To summarise, the results of this investigation are, with a few notable exceptions, in accordance with the background of pertinent laboratory and ecological studies; the experiments emphasise the importance of sound behavioural knowledge to the consideration of problems concerning fish and fisheries.
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APPENDIX

SPECIFICATIONS OF APPARATUS
AND EQUIPMENT USED IN THE
INVESTIGATION
A.1

Introduction

Most of the equipment used in this investigation was designed and built specifically for the experiments. Because of the problems posed by a supply of tap-water which was both heavily chlorinated and frequently turned off without warning it was necessary to build holding and experimental tanks that depended upon recirculation of water. The ways in which the water was purified varied according to the piece of equipment in question.

As several sets of equipment were used for more than one experiment full descriptions and specifications are given below to avoid replication at the beginning of individual experiments.

A.2

For OE1 and Small-tank Preliminary Experiment of BE3

A pair of angle iron/glass tanks joined to each other and to a circulating/cooling apparatus.

a) External dimensions: each tank, 90cm long, 30cm wide and 38cm high.

b) Water depth: 17cm in BE1, 15cm in BE3 Preliminary Experiment.

c) Fish-proofing (to prevent fish escaping from the experimental tanks): Screens of 3mm rigid P.V.C. were cut to fit each end of the tanks and were perforated with 5mm holes, allowing circulation of water but preventing fish from escaping. These screens also visually isolated the two tanks.

d) Lighting: Daylight.

e) Recirculation system: The water was circulated through the two tanks, which were connected to each other by two 2cm diameter pipes situated 5cm above the bottom, and 5cm from the sides of the tanks, by means of a Churchill chiller/circulator. Flow rate varied from 100 to 150 litres.
f) Filtration of water: Between the chiller/circulator and the first tank inlet the water passed through a polymer wool/activated charcoal filter, housed in a glass tube, diameter 4.3cm, length 50cm. The gradual blocking of this filter caused the variation in flow rates. The filter was renewed between runs in both experiments.

Aeration was provided by aquarium aerating stones, one of which was placed between the end of the tank and the upstream screen in each tank, connected to a 'Hy-Flo' air pump.

g) Temperature control: Churchill chiller, temperature in both experiments maintained at 15°C.

h) Support: Tanks were supported on a framework of Dexion angle iron, sides 4 and 6cm.

A.3

For BF2

A series of ten angle iron/glass tanks was used in this experiment.

a) External dimensions: Each tank was nominally 75cm long, 30cm wide and 30cm high.

b) Water volume: Each tank contained between 45 and 47.5 litres.

c) Fish-proofing: Inlets and outlets of the tanks were fitted with guards made from nylon monofilament which prevented fish from entering the pipes. All tanks were covered with glass sheets, leaving spaces only for air lines and siphons.

d) Lighting: Light was supplied by two 5ft daylight fluorescent tubes fixed approximately 50cm above the water surface and operating on a 12 hour photoperiod. The lights were supplementary to natural daylight.
The tanks were visually isolated from one another by sheets of 3mm marine plywood.

\text{e) Recirculation systems: All of the tanks were connected to their neighbours with 15mm diameter siphon tubes and water was recirculated by means of a system of reservoirs and constant-head tanks, driven by an electric pump. Flow rate was 32.5 litres per hour.}

\text{f) Filtration of waters: The circulating water was passed through a polymer wool/activated charcoal filter of the same type as used in BE1 (4.3cm diameter, 50cm long) which was renewed twice weekly during the experiment. Each tank was aerated individually.}

Three times per week the tanks were cleaned by siphoning out approximately 40 litres of water and this was replaced by the same volume of tap water, which had been vigorously aerated for at least two days. Consequently the water in the system was, in effect, changed completely every four or five weeks.

A by-pass system of one of the constant head tanks meant that the water entering the series of tanks was thoroughly aerated.

\text{g) Temperature controls: No attempt was made to control water temperature in BE2.}

\text{h) Supports: The system was supported on a Nexion frame with the tanks resting, in sets of three, in galvanised trays (1m square approximately) which channelled any overflow water to waste.}

A4

\text{For the growth experiment and carrying capacity experiments}

A single large tank divided longitudinally into two identical channels. This tank was built from grey 9mm rigid P.V.C. and was sealed with Dow-Corning Silicone-Rubber sealant.}

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a) External dimensions: 244cm long, 91.5cm wide and 30.5cm high.

b) Dimensions of channels: For the growth experiment the size of each channel was 236 x 44cm. The overall length was shortened because of the baffles at the inlets and outlets.

For the carrying capacity experiments the length of the channels was reduced further as up- and downstream dams were fixed approximately 15cm from each end. The size of each channel in these experiments was 204 by 44cm. The upstream dams were 16cm high, the downstream ones 13cm.

c) Water depths: This depended upon the experiment being performed and so depths are described in the individual experiments.

d) Fish-proofing: Fish were prevented from leaving the channels (traps in the carrying capacity experiment) by baffles or 'false ends' to the channels. These were made of the same material as the rest of the tank and were perforated with 2mm diameter holes.

For stage 3 of the third carrying capacity experiment, when very small fish were used, the edges of the screens, dams and dividing wall were fitted with self-adhesive strips of foam draught-excluder which completely isolated the various compartments of the tank, preventing the fish from escaping through the tiny irregularities caused by cutting the P.V.C. sheet to size when building the tanks.

e) Lighting: For the growth experiment the tank was illuminated by daylight.

In the carrying capacity experiment daylight was excluded from the tank by a black polythene 'tent' and the channels were lit by a single 15 watt 5ft. daylight fluorescent tube suspended approximately 1m above the water surface. A 12 hour photoperiod was used in the second carrying capacity experiment and an 8.5/15.5 light/dark regime in stage 3 of the third carrying capacity experiment.
f) Recirculation system: Water was circulated by means of an electric pump, a system of reservoirs and a constant-head tank.

Flow rate through the channels was adjustable by taps and during the growth experiment and the first and second carrying capacity experiments the flow rate was about 575 litres per hour. This was increased to 650 litres per hour for stage 3 of the third carrying capacity experiment.

g) Filtration of water: During recirculation, part of the water overflowing from the constant-head tank was passed through a pair of activated charcoal filters before returning to the reservoir tank. The vigorous aeration during recirculation and the large water volume/fish load ratio also helped to prevent contamination of the water.

Any water removed when the tanks were cleaned was replaced with aged tap-water.

h) Temperature control: A refrigeration unit was connected to a set of cold-plates in one of the reservoirs. This apparatus was used only in the growth experiment when a maximum temperature of 15°C was maintained.

i) Support: The main tanks, reservoirs and constant-head tank were supported on a free-standing Dexion frame. The refrigeration unit was floor-mounted to reduce vibration in the tanks.

This apparatus is shown in fig. A.1.

A.5

For RE3 and Stages 1 and 2 of the third carrying capacity experiment

A pair of tanks built to the same specifications and housed in a common Dexion framework. Materials used were 7mm rigid P.V.C., grey in colour, and transparent 9mm perspex. The tanks were sealed with Dow-Corning Silicons Rubber sealant.

e) External dimensions: 245cm long, 57cm wide and 59cm high.
Fig A1 Equipment used in the carrying capacity and growth experiments
Top: Side elevation  Bottom: Plan view  Dexion frames omitted

C Chiller  CD Central division  CE Chiller element  C1, C2 Channels 1 & 2
CHO Constant head outlet  DB Downstream baffle  DD Downstream dam
DT Downstream trap  F Activated charcoal filter  G Gravity-controlled
flow to channels  HT Header tank  L Light strip  O Outlets from channels
P Pump  R1, R2 Reservoirs  T Tap-controlled flow to channels
UB Upstream baffle  UD Upstream dam  UT Upstream trap  WL Water level
b) Water depths: A mean of 31.5cm for BC3 and 13.5cm in stages 1 and 2 of the third carrying capacity experiment.

c) Fish-proofings: Screens made of the same 7mm P.V.C. as the tanks were placed 7cm from the upstream end (inlet) of the tank and 13cm from the downstream end of the tank. Water flowed through the screens via 1cm slits cut from the bottom of the screens to above the water level. The screens alone were sufficient to prevent fish from escaping in BC3 but when the much smaller fish were used in stages 1 and 2 of the third carrying capacity experiment the edges of the screens were sealed with self-adhesive foam draught-excluding strip, as in the tank for stage 3 of the same experiment.

d) Lighting: Daylight was excluded from the room and illumination provided by a single 100 watt incandescent bulb situated in the ceiling of the room, between the two tanks. No time switch was fitted to this light. A manually operated photoperiod of 8.5/15.5 hours light/dark was maintained in both experiments.

e) Recirculation system: Each tank had exactly the same water recirculation system, composed of a header-tank with tap-controlled flow into the tanks, a drainage reservoir and an electric pump.

Water flow through the system was approximately 1200 litres per hour.

f) Filtration of water: Because of the high ratio of water volume to fish load in these tanks no chemical filtration of the water was needed. By allowing a 15cm drop between the outlet and the water level of the drainage reservoir, constant vigorous aeration was maintained, which was sufficient to prevent the accumulation of dissolved ammonia. Water removed by siphoning was replaced with aged tap-water.

g) Temperature control: Each tank was cooled by a Churchill chiller
which pumped a water/alcohol mixture at between -2 and -10°C through a series of ten glass tubes, internal diameter 5mm, length 300cm, submerged in the header tanks.

h) Support: The tanks and header tanks were supported on a Dexion frame. Pumps and drainage reservoirs were floor-mounted to reduce vibration in the tanks. The Churchill chillers were situated in an adjacent room, to avoid heating the tank-room, and were 'plumbed-in' to the system through the wall.

i) Observation chamber: The Dexion frames were built so as to form an observation chamber between the two tanks. The chamber was 120cm high, 60cm wide and the same length as the tanks. By using black polythene sheeting it was arranged that the only light entering the chamber was that passing through the perspex sides of the tanks.

This apparatus is shown in Fig. A.2.

A.6

Stock Tanks

Stock fish were kept in three outside tanks. Two tanks were black P.V.C. cold-water cisterns, the third was a white, rectangular polythene tank.

a) Dimensions: Round tank: diameter 85cm, height 68cm. Rectangular tank: 105cm long, 91cm wide and 68cm high.

b) Water depths: Rectangular tank: 53.5cm, first circular tank, 47.5cm; second circular tank, 42.0cm.

c) Fish-proofing: Fish were prevented from leaving the tanks via the water outlet by means of screened outlet pipes. The pipes were made from half an inch diameter ABS tubing, 25cm long, perforated with 3mm holes. As the outlet itself was threaded, the pipe was simply screwed on to the outlet, allowing easy removal for cleaning.
Fig. A2  Design of tanks used in BE3 and stages 1 & 2 of the third carrying capacity experiment.

B Batties, C Cooling coil, CHO Constant head outlet, HT Header tank, O Outlet pipe, 5cm diameter, variable height

P Pump, R Reservoir, T Tap-controlled flow to tank, WL Water level
d) Lighting: Originally the tanks were left open, subject to daylight but this situation was unsatisfactory as dense blooms of green algae grow, making the catching of fish from the tanks impossible. To prevent growth of algae, the tanks were covered with black polythene sheeting which reduced the light intensity. The sheeting was supported on a tubular aluminium frame over the circular tanks and by corrugated clear P.V.C. roofing material over the rectangular tank.

e) Recirculation system: Water was constantly recirculated by an electric pump. Flow rates depended on the distance of the tank in question from the pump and were, starting with the tank nearest the pump, 205, 190, and 120 litres per hour.

f) Filtration: When the stock tanks were built, provision was made for an activated charcoal filter within the pump reservoir but this proved impractical as it became blocked very quickly, stopping recirculation.

The chemical filter in the pump reservoir was replaced by a sheet of 0.1mm mesh nylon cloth (Nybolt) to act as a mechanical filter, and activated charcoal/polymer wool air lift filters were placed in each of the tanks. This, combined with the aeration received during recirculation was adequate.

g) Temperature control: Temperature control was used only when the ambient temperature was very high or very low.

In hot weather a water/alcohol coolant at -2°C was pumped through a glass coil, 5mm diameter, total length 2.5m immersed in the pump reservoir.

In winter, when there was a danger of the water in the recirculation system freezing, a 100 watt aquarium heater was placed in the pump reservoir and set to operate between 7 and 15°C. This prevented the water from getting any colder than 2°C, despite heavy overnight frosts.
Feeding Apparatus for GE3 and Carrying Capacity Experiment Stages 1 and 2

In order to be able to feed the fish in GE3 and stages 1 and 2 of the third carrying capacity experiment without disturbing them, a remote-control feeder was built. The feeder was made from 12mm diameter ABS tube from which food pellets were pushed by a brass piston of the same diameter, activated by means of a bicycle brake cable. The whole apparatus was mounted on a wooden block which could be bolted to the Dexion tank frame in the desired position.

This piece of equipment is shown in fig. A.3.
Fig A3 Remote-control feeding apparatus
Top; feeder unit  Bottom; operating unit
B Plywood base  b bolt to fix feeder unit to Dexion frame  C Plastic-sheathed steel cable  Cl Clamp holding cable to base  D Dexion tank-frame
F Food hopper  H Handle fixed to end of cable  P Brass piston, dashed lines indicate limit of travel  T Brass tube with slot for travel of handle