THE EFFECTS OF PRIOR DEPTH EXPERIENCE, FEEDING, AGE AND LIGHT ON DEPTH PREFERENCE IN HAPLOCHROMIS BURTONI

Dissertation for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
TRACY SUSAN CARTER
1975

This is to certify that the

thesis entitled

THE EFFECTS OF PRIOR DEPTH EXPERIENCE,
FEEDING, AGE AND LIGHT ON DEPTH
PREFERENCE IN HAPLOCHROMIS BURTONI

presented by

TRACY SUSAN CARTER

has been accepted towards fulfillment
of the requirements for

PHD degree in ZOOLOGY

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Date JANUARY 9, 1975

O-7639

#071

ABSTRACT

THE EFFECTS OF PRIOR DEPTH EXPERIENCE, FEEDING, AGE AND LIGHT ON DEPTH PREFERENCE IN *HAPLOCHROMIS BURTONI*

By

Tracy Susan Carter

The role of prior experience on depth selection in the cichlid fish, *Haplochromis burtoni*, was investigated in this study. Within the investigation the effects of age and feeding were determined. The fish were reared in either deep or shallow water for six or twelve months. Individuals were tested in experimental aquaria that consisted of a series of steps ranging in depth from the depth of the shallow conditioning tanks to the depth of the deep conditioning tanks. The fish's position was noted every fifteen seconds for ten minutes a day for three days. Swim bouts and feeding movements were also recorded. Fed fish were fed one hour before testing; unfed fish were not fed during the experiment.

Shallow-raised, 12-month fish were found to appear significantly more often than deep-raised, 12-month fish, on areas that were directly associated with the substrate. These fish made fewer swim bouts and many more feeding movements than deep-raised fish.

Deep-raised, 12-month fish occurred in open waters and ranged in the longest vertical column significantly more often than shallow-raised, 12-month fish. They were also in the shallow water areas more often on day one. These behaviors were suggested to be associated with the earlier experience of the fish and its response to the degree of novelty of the experimental tank situation.

When fed fish were compared with unfed fish it was found that the fed fish were occupying the substrate-associated areas. They also made more feeding movements and fewer swim bouts than unfed fish. Unfed fish were in open waters and shallow water areas more often than fed fish. These reactions were associated with food-seeking and feeding responses.

The interaction between experience and feeding situation was analysed. Unfed fish were little influenced by prior experience. Fed fish were affected by early experience. Deep-raised, fed fish were in open waters most often of all groups; shallow-raised, fed fish were there least often. Shallow-raised, fed fish occurred most often of all groups in the substrate associated areas; deep-raised, fed fish occurred in these areas least often. It, therefore, appears that feeding reinforces habitat imprinting while hunger overrides it.

When 6-month fish were compared with 12-month fish, it was found that 6-month fish were in substrate-associated areas while 12-month fish occurred more often in open water and in shallow water areas.

Regardless of age, all shallow-raised fish were substrate-associated while all deep-raised fish appeared significantly more often in open waters.

When the interaction of age and prior experience was analysed, there was no influence of age on deep-raised fish. Age very much influenced the behavior of shallow-raised fish. Shallow-raised, 6-month fish were the group most closely associated with the substrate; shallow-raised, 12-month fish were found in open waters and along the top surface of the water. Possible explanations for these differences were discussed.

A second experiment examined the reaction of fish to light in a choice situation between lighted and darkened areas of the same experimental aquaria used in the first experiment. For the deep-dark testing, the deep halves of the aquaria were darkened. The shallow-dark tests had the shallow halves of the aquaria darkened. A third test, the all-lit test, was made under conditions where the entire aquarium was lit.

Shallow-dark tested fish avoided the shallow-dark region, the light-dark boundary and the shallow water areas. They occupied the deep areas of the aquaria. Deep-dark tested fish showed no differences in selection of either half of the aquaria but did avoid the light-dark boundary.

When shallow-dark tested fish were compared to all-lit tested fish it was found that all-lit tested fish occurred

in the shallow water region much more frequently than shallow-dark tested fish. In a comparison of deep-dark tested fish with all-lit tested fish, all-lit tested fish were shown to occur in shallow water areas more frequently, while deep-dark fish occurred in the deep water areas more often.

In a comparison of deep-dark tested fish with shallow-dark tested fish, no difference was found in the amount of time spent in the deep water areas. Deep-dark tested fish appeared more often in the shallow water areas. Possible explanations for the behavior of the fish were discussed.

The applied aspects of the research were discussed and future study was proposed.

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By

Tracy Susan Carter

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1975

To my parents, Alfredda S. Phelps Carter and Max Martin Carter, I love them and I miss them.

ACKNOWLEDGEMENTS

I wish to extend my sincere appreciation to Dr. James C. Braddock who served as my major professor and allowed me the independence to study what interested me. I would like to thank Dr. Eugene Roelofs for his thoughtful criticisms and comments and for serving as a committee member. I would also like to thank Dr. M. M. Hensley and Dr. Rollin Baker for serving as committee members.

The kind assistances of the Zoology Department, its secretaries and Mr. James Lucas was greatly appreciated. Dr. Howard Teitelbaum was most helpful with support for computer time and Mr. Steve Olejnik was very helpful with the computer setup.

Special thanks must go to my good friend Signe Nelson for the hours she spent over a typewriter for me, she unselfishly gave her time and efforts to me. I would like to thank my friends, Ripalda Krasnoborski, Karen Kovach, and Dr. Lou Betty Rood for their unfailing faith in me.

And lastly, I would like to thank my friend Dick Mikula, who allowed every weekend, every day we were together, to be broken up by my research and animal care time. A kinder, more patient person, I'll never meet.

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INTRODUCTION

The experiments described in this thesis were designed to help answer certain questions about habitat selection and its relationship to water depth preference. The first experiment tested for the effect of early depth experience on later depth preference. Within this experiment the effect of hunger was studied. Age is also considered an important determinant so it too was tested.

One of the most important elements of depth of water is believed to be light. Just how important light is for depth selection has not yet been determined. I designed a set of experiments to test what effect light has on depth choice. The natural situation is for light intensity to decrease as water depth increases. I wanted to know how important this phenomenon was in determining where a fish would occur. Therefore fish were observed in the normal situation, with the normal situation enhanced and with that situation reversed. The reversal made the shallow water dark and the deep water lighter. The following paragraphs describe some of the literature reviewed in the process of designing these tests.

For years it has been noted that animals are located in specific areas. The parameters of distribution have been recorded for many types of animals; for example, Duronslet et al. (1972) studied the distribution of shrimp, Hallam (1959) described the habitat structure of four species of fish. Various factors will lead to change of location. Narver (1969) as well as many others (Blaxter and Parrish, 1958; Schwassman, 1960; Brawn, 1960; Stickney, 1972; Alabaster and Robertson, 1961; Cushing, 1951; Harris and Wolfe, 1955; Pinhorn and Andrews, 1965; and Costa and Cummins, 1969) have noted the diel movements of zooplankton and fish.

The location of a species in a certain area is dependent on many factors. Predation, starvation, exposure and other factors play important roles in determining where an animal can occur. Animals must therefore selectively choose areas of the environment that will best insure their survival. Factors such as available food, light and temperature are often a major concern. Selection does not occur on the basis of a single parameter but rather it is the interaction of factors which is important. Harris and Wolfe (1955) studied the vertical movements of Daphnia in relation to light. Sexton and Ortleb (1966) noted that several factors (water depth, cover and current) were important for the selection of oviposition sites by a leptodactylid frog. Heatwole (1961) observed the effects of temperature and humidity on the location of the wood frog. He (1962) also recorded factors influencing the distribution of *Plethodon cinereus* and stated that the salamander's behavioral response to the physical structure was important and that the whole environmental complex affected vertical and horizontal seasonal migrations. Research by Kendeigh (1945) on community selection of birds in New York correlated selection with avoidance of high light intensities and restriction of free flight. He showed that these birds preferred foliage of a certain size, shape and arrangement of leaves rather than specific foliage types per se. Wetzel (1958) described the succession of mammals that occurs with the changing habitat of midwestern floodplains.

There have been many studies on fish that correlate habitat occurrence with one or more variables. Woodhead (1964) did an extensive study of the effects of light on the distribution of demersal fish of the North Atlantic. He (1955) further noted the reactions of herring larvae to light by recording their vertical movements. Baker (1971) recorded that the presence or absence of *Elodea* strongly affected the habitat selection of the four-spine stickleback. The effects of light on temperature selection in speckled trout were studied by Sullivan and Fisher (1954). They observed that temperature selection was more precise at low light intensities.

Change in location can be due to change in physiological state. Insects find specific oviposition sites when they are ready to lay their eggs. Sexton and Ortleb (1966) recorded the type of environment chosen by the leptodactylid frog for oviposition. The features of this habitat differ from the normal habitat where non-reproducing frogs were found. Hunsaker and Crawford (1964) measured the parameters of the spawning sites of largemouth bass; these are quite distinct and separate from areas selected at other times. Of course one would usually expect to find a hungry animal in a different place than a sleeping or courting animal.

The social status of an individual can affect its behavior and therefore its choice of an area. A very submissive fish will usually be found motionless at the top of an aquarium whereas a dominant fish will be found occupying a large part of the bottom of the aquarium actively excluding other fish.

Reproductive state affects the microhabitat distribution of animals. Nesting female birds are sometimes found in one area of a habitat while the males are found in another (Morse, 1968). A lek of courting birds gathers in a specific open type of area which is very much different from the microhabitat chosen by a bird under attack. Very few wild mammals have been observed giving birth (except of course those that have dens or nests), which leads one to expect that the choice of birthplace is again quite different from the usual location.

Age and sex can have a definite effect on the orientation of many animals. Dolley and Golden (1947) reported the reaction to light of the invertebrate *Eristalis tenax* and the fact that, depending on age and sex, the animals could be either photopositive or photonegative. This selection has been shown in flagellates (Massart, 1891), leeches (Kanda, 1919), water spiders (Mast, 1911), barnacles (Rose, 1929), Mayfly nymphs (Allee and Stein, 1918), and many others. Hadley (1908) studied the behavior of the American lobster and discovered that larvae are photopositive for two days after hatching, photonegative in the second and third stage of development, but become photopositive again before molting, and in the fourth and later stages they are photonegative. Fast and Momot (1973) found that although crayfish exhibit seasonal depth distribution based on sex, age and water temperature, if the lakes were artificially aerated and therefore thermally destratified, both sexes were distributed equally throughout the lake. They postulated that the social aggression of large males forced females into deeper, cooler water and that this aggression was temperature related. Kwain and McCrimmon (1969 and 1967) demonstrated the effects of age on bottom color selection by rainbow trout. Ali (1959) showed that because older salmon have longer light adaptation times, they are located in areas of a stream at different times than younger fish.

Growth also affects the distribution of animals. Sale (1969) demonstrated that the juvenile manini fish, Acanthurus trioslegus sandvicensis, move towards deeper water as they grow. Halliday (1967) observed the effect of growth on the vertical distribution of glacier lantern fish. Enders (1974) studied the web height of orb-web spiders and learned that vertical stratification occurred due to size differences.

Internal and external factors interact to cause an animal to react in a specific way. Kapoor (1971) learned that the locomotory pattern of fish changes under different levels of illumination. Stickney (1972) studied this phenomena in juvenile herring. Sale (1968) discovered that corals affect the dispersion of pomacentrid fish. Varanelli and McCleave (1974) observed the locomotory activity of Atlantic salmon in relation to light and a weak magnetic field. Brunel (1964) did research on food as a factor or indicator of vertical migration in cod. "Vertical migration of shrimp: a feeding and dispersal mechanism" was studied by Pearcy (1970). The effects of negative buoyancy on the behavior of bluegills was noted by Gallepp and Magnum (1972). Saunders (1966) observed the buoyancy adjustments of Atlantic salmon parr in relation to changing water velocity, and Peterson (1971) noted the effect of barometric pressure on their spawning behavior.

Habitat selection is the term used to describe active selection by an animal of a specific habitat. It is primarily influenced by genetics. Hildén (1965) stated that birds are guided to breeding stations primarily by an innate reaction released by environmental stimuli and that the threshold for action is dependent on internal motivation. However she continues to say that it has long been understood that psychological factors play a role in habitat selection by birds.

One of the earliest works on habitat selection is by Harris in 1952. He found that, as expected, wild caught *Peromyscus maniculatus bairdi* chose an artificial habitat that resembled the open fields where they naturally occur. First generation *Peromyscus maniculatus gracilis* selected tree trunks which appear to most closely resemble their natural habitat of hardwood forest. Laboratory bred subspecies also selected the habitat that they would normally inhabit in the wild state. Interestingly, *bairdi-gracilis* hybrids selected grass, indicating that this is more powerfully selected for than woodlands. Harris concluded that habitat selection was genetically based; however, he did not investigate the possibility that learning might also be involved.

Wecker (1963) decided to examine the possible effects of learning on habitat selection. Following Harris's work he used *Peromyscus maniculatus bairdi* and found that field-caught adults and their offspring selected a field habitat over a woodlot when he gave them a choice situation. Early experience, for the first generation young in the woods or laboratory, was not sufficient to reverse the normal attraction to a field habitat. Prior experience in a field habitat reinforced the innate preference but was not necessary for the response. Laboratory rearing of 12-20 generations of mice caused a loss of the innate preference for field. They did, however, retain the capacity for learning which allowed them to select field conditions if exposed to them at an early age.

Klopfer (1963, 1965 and 1967) and Klopfer and Hailman (1965) investigated the importance of prior habitat experience on later habitat selection in chipping sparrows and blue tanagers. Field-caught or hand-reared chipping sparrows displayed a preference for pine foliage over oak, but birds raised in the presence of oak foliage showed a decreased preference for pine. Later all the birds were put in an outdoor pen with oak. At sexual maturity all birds preferred pine when retested. These results do not necessarily show that the preference for pine at maturity is not in innate mechanism. A test following King's (1958) parameters would lend insight to this question.

The effect of early experience on tadpoles was demonstrated by Weins (1970, 1972). Rana aurora tadpoles that were reared in featureless or square-patterned environments showed no preference for either substrate. Striped-reared individuals however showed a significant preference for striped substrate. Further experiments indicated that the preference was retained through a time of isolation from the rearing substrate and during periods of growth, neural maturation and reorganization. Tadpoles just beginning to metamorphose established a preference as quickly and as strongly as individuals midway through larval development. Weins found that Rana cascadae tadpoles raised in a square-patterned habitat demonstrated a significant preference for the square-patterned substrate; however, tadpoles reared in featureless or striped-patterned environments showed no preference for either square or striped substrata. This preference is opposite to that of R. aurora tadpoles. The difference in preference of these two species may be due to the difference in habitats in which the tadpoles normally mature. R. aurora occur in ponds where stems of the vegetation give a striped appearance and cast striped shadows. R. cascadae habitat consists of rocks and clumps of vegetation, that is, a patchy appearance.

An interesting investigation by Sargent (1965) showed an interaction of experience and genetics in the zebra finch. Previous nesting experience affected later nesting behavior. The birds were given experience with a certain color of nesting material, type of nest substrate and nest location. The later choice of nest color was found to depend not only on experience but on species-typical color also. If the birds were raised on green or brown materials (typical nest colors) they later chose green or brown respectively. But, if birds were raised on red nesting materials, an extremely atypical nest color, they later chose either green or brown nesting materials.

Sale (1971) noted that two populations of a coral-reef fish, *Dascyllus aruanus* were associated with two different species of coral. In a choice situation both populations chose the type of coral that they were found with in the field. This research supports the concept of learning in fish. Several other studies of learning in fish have been conducted. Aronson's (1951) study of a gobiid fish, *Bathygobius soporator*, suggests that these fish learn the local substrate configuration at high tide and use this knowledge later to move by jumping from one tide pool to another at low tide. Work by Hasler (1956 and 1966) also supports the probability of fish using learning for orientation.

In view of all of this information I designed a set of experiments to determine the effects of certain parameters on depth preference in fish. To my knowledge the effect of early experience on depth distribution has never been studied, and this is partially why I chose to do so. A study of depth selection could have significance in fisheries work. Buss et al. (1970) have shown the advantages of raising trout in vertical units. The effects of light on depth preference

CORRECTION

Page 11, paragraph two, line seven should read: They pointed out that the presence or absence of the swimbladder is one of the most important factors affecting fish distribution. Thus, while fish with closed swimbladders are restricted in their vertical movements (Moreau, 1876; Jones, 1951 and 1952; and Jones and Marshall, 1953), those with an open swimbladder live mostly near the air-water surface where they can swallow air bubbles from the air while fish without a swimbladder move with difficulty when off the bottom.

appear to be quite important, however, no one has ever studied these effects in a choice situation. Therefore, I decided to examine the question.

A fish's response to depth depends on several factors including whether the fish has a swimbladder or not, and, if it has one, whether it is a physoclist (closed swimbladder with no connection to the stomach) or a physostom (open swimbladder attached to the stomach). Jones and Marshall (1953) reviewed the swimbladder and its functions. They pointed out that the presence or absence of the swimbladder are restricted in their vertical movements (Moreau, 1876; Jones, 1951 and 1952; and Jones and Marshall, 1953), those with an open swimbladder live mostly near the airwater surface where they can swallow air bubbles from the air, while fish without a swimbladder move with difficulty when off the bottom. It seems that the loss of the swimbladder is associated with a bottom living habit. Jones and Marshall (1953) concluded that in fresh water the number of species of physostomatous teleosts (open swimbladder) will surpass that of physoclists, but in the sea the latter are strikingly predominant. This may be attributed to an evolutionary significance since increase in the density of the environment takes place at sea.

Since the swimbladder acts as a hydrostatic organ, the fish is able to compensate for the density change when it moves from one level to another by adjusting the volume of the swimbladder. In physoclists adjustment takes place by secretion or absorption of gas into or from the swimbladder, while in physostomes the excess gas is released through the pneumatic duct and air bubbles are swallowed from the air in order to replace gas lost from the swimbladder. As physostomes secrete gas slowly they must depend on the surface to replace the lost gas from the bladder (Jones and Marshall, 1953 and Bishai, 1961). Jones and Marshall (1953) concluded that most freshwater species live well within the limit of pressure.

MATERIALS AND METHODS

Experimental Animals

The cichild fish Haplochromis burtoni (Günther) was chosen as my test animal for several reasons: the fish is small enough to show a proportional response to the depth range of the experimental aquaria, reaches sexual maturity early (6-8 months, personal observation), and is easy to raise and breed. Also Fryer and Iles (1972) reported that H. burtoni is found in shallow waters and swamps so they would be naturally adapted to the parameters of the experiments.

When I dissected some H. burtoni I discovered that they had swimbladders with well developed retia mirabilia and gas glands. Jones and Marshall (1963) pointed out that gas glands consisting of many layers of cells are found in fish groups which include Perciformes from which Haplochromis evolved. The capacity for secreting gas into the bladder is correlated with the degree to which the lining epithelium is differentiated into glandular tissue, as well as the presence of retia mirabilia. Jacobs (1934) pointed out that fish whose gas gland and rete mirabile are well developed can make appreciable adjustments to the swimbladder volume in a matter of hours. The Haplochromis burtoni were acclimated for 24 hours.

The individuals used were from a local fish aquarist. The species was identified by Dr. R. Miller, an ichthyologist at the University of Michigan at Ann Arbor, Michigan. The fish used in the study were at least third generation laboratory stock.

Rearing Conditions

The fish were raised in 76-liter (20 gallon) aquaria. All had natural gravel on the bottom. The water was filtered by bubble-up or Le-Bern outside filters and aerated with airstones.

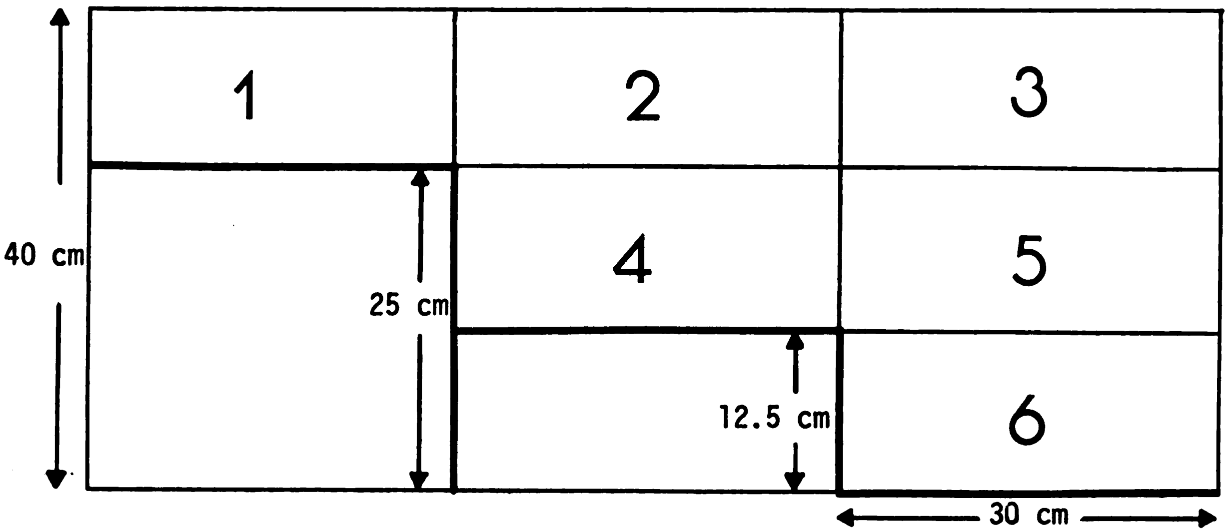
Four grams of marine salt were added to each gallon of water. Tap water that was run through an activated charcoal filter and temperature acclimated was used in all aquaria. A water temperature of 25° ± 1°C was maintained by a room air conditioner and heater. A fifteen-hour on, nine-hour off photoperiod was used. The lights came on at 700 hours and went off at 2200 hours. Lighting was by fluorescent ceiling light and incandescent lights suspended above the aquaria.

The light intensity measured 300-500 lux. at the bottom of the aquaria. The aquaria were covered with glass tops. The fish were fed BiOrell flake food once daily at approximately 1400 hours.

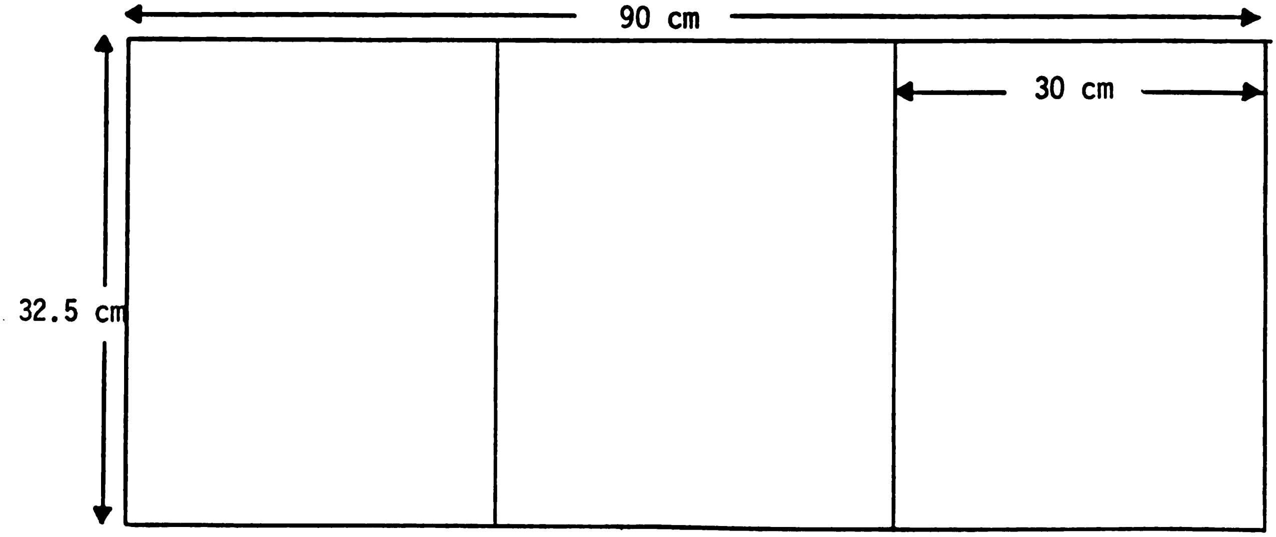
Mouth-brooding females from four breeding aquaria were used to supply young. A female holding eggs or wriggler-stage young in her mouth was netted from a breeding aquarium and placed in a conditioning aquarium that had a specific water depth. Several days after the young became free-swimming the female was removed. The depth of the water in the conditioning aquaria was maintained by daily addition of water. The water depth was either 37.5 cm. (15 inches) for deep-raised fish or 12.5 cm. (5 inches) for shallow-raised fish. The fish used in the light experiment were also raised at 12.5 cm. water depth.

Experimental Aquaria

The three experimental aquaria (Figure 1) were standard 114-liter (30 gallon) capacity. They measured 90 cm. (36 in.) X 32.5 cm. (13 in.) X 40 cm. (16 in.). All sides but the front were painted with grey paint to shut out disturbances. The aquaria were divided into three steps. These steps were marked off so as to divide the aquaria into six equal-sized areas (Figure 2). Each green plexiglas platform measured 30 cm. X 30.625 cm. Thus, each depth received a uniform-shaped bottom surface. For each green plexiglas step there was a 12.5 cm. (5 in.) depth difference. Therefore, the plexiglas walls measured 12.5 cm. X 30.625 cm. and 25 cm. X 30.625 cm. giving three water depths of 12.5 cm., 25 cm. and 37.5 cm. (5 in., 10 in. and 15 in.). As mentioned



SIDE VIEW



TOP VIEW

Figure 1.--Diagram of the experimental tank.

Figure 2.--Photograph of the experimental tank.

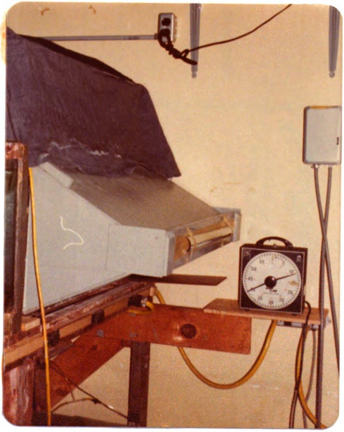


Figure 3.--Photograph of the viewing apparatus.

earlier, the fish were raised in either 12.5 cm. or 37.5 cm. of water so these were either the deepest or shallowest depths of the experimental aquaria.

For the experiments I wanted to measure the reaction of the fish at a range of depth that was neither too deep for them to compensate for quickly nor to slight for them to detect. The depths of the experimental aquaria were well within the range for quick compensation. McCutcheon (1958) demonstrated that teleosts could compensate for slight changes very rapidly, e.g., .5 cm. in .5 to 2.0 sec. He also showed (1966) that teleosts were sensitive to (aware of) very small pressure changes. The experimental aquaria fulfilled these requirements.

The bottom surfaces were covered with the same natural aquarium gravel as used in the conditioning aquaria. The areas of the aquaria were divided off across the front and back with strips of tape. An airstone was suspended in each tank.

The fish were observed through a viewing apparatus (Figure 3). The screen of the viewer was covered with one-way plastic to conceal the observer. To further exclude outside light, dark denim covered the entire experimental area.

The test aquaria were illuminated by fluorescent lights located directly above. The light intensity measured 300 lux in Area 1, 500 lux in Area 4 and 250 lux in Area 6.

The photoperiod was the same as in the conditioning aquaria, as was the temperature. The same water and salt proportions as in the conditioning aquaria were also used.

To control for possible left or right orientation the aquaria were set up in opposite directions. Aquaria 2 and 3 were designed so that area number six is to the left as viewed. Aquarium 1 had Area 6 to the right.

Procedures

Each fish was tested individually. The fish was netted, measured, sexed and introduced into a testing aquarium. Size at testing was between 2.5 cm. and 4.9 cm. for 12-month fish and 2.4 cm. and 3.0 cm. for 6-month fish. Twenty-four hours after introduction the first observation took place. The observer sat in front of the viewer with the dark denim covering her. There was a pause of ten minutes before recording took place to allow the fish to adjust to any slight disturbances caused by the observer's positioning. Observations were made by recording the fish's position every fifteen seconds for ten minutes. The observer marked which area the fish occupied. The position of a fish was pinpointed by the specific location of the fish's eye. Also recorded were any feeding movements a fish made during the 15-second period and any swim bouts that occurred. A feeding movement was any mouth movement made by the fish, that appeared as if the fish was eating. A swim bout was defined as any rapid succession of movements which did not simply move a fish from one area to another but rather consisted of a type of exercise. Each fish was observed for three days after which it was removed; water was added to the experimental aquarium; and any misplaced gravel was smoothed. No mouth-brooding females were used.

Experiment I

This experiment was designed to test the effect of rearing depth on subsequent depth preference. Within the experiment I tested the effects of feeding and age. There were six experimental groups. The fish were reared in shallow (12.5 cm.) water or deep (37.5 cm.) water. There were fifteen fish in each group.

Group I to be referred to as DN was deep-raised to twelve months of age before testing and was not fed during the experiment. Group II, designated DF, was also deep-raised for a year but was fed one hour before each test. Group III (SN) was shallow-raised for 12 months and not fed during the testing, and Group IV (SF) was also shallow-raised for a year but was fed before each test.

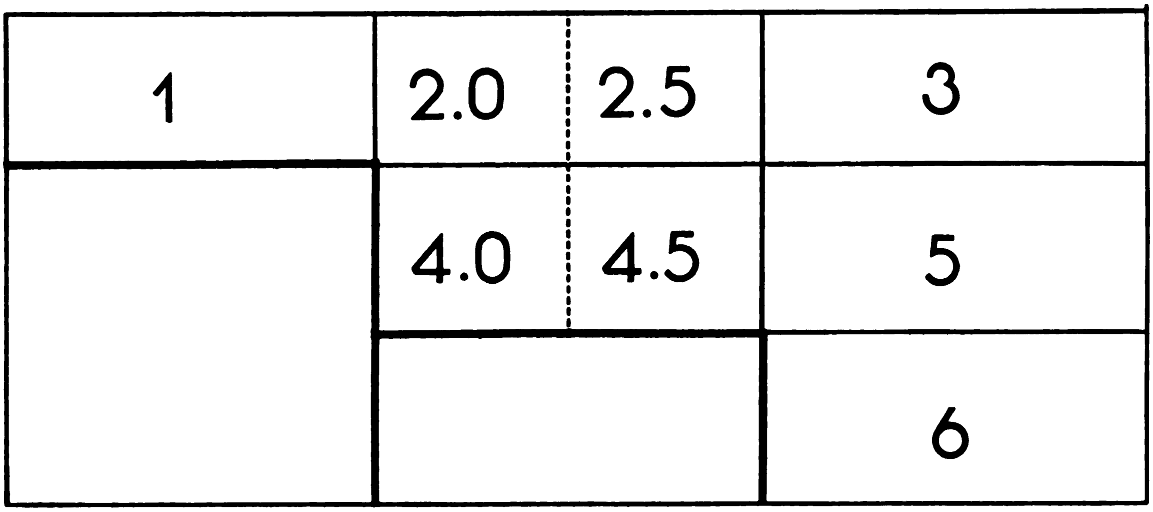
Groups V and VI, designated as 6-month DN and 6-month SN respectively, were tested at six months of age and not fed during the experiment. Group V was deep-raised and Group VI was shallow-raised.

Experiment II

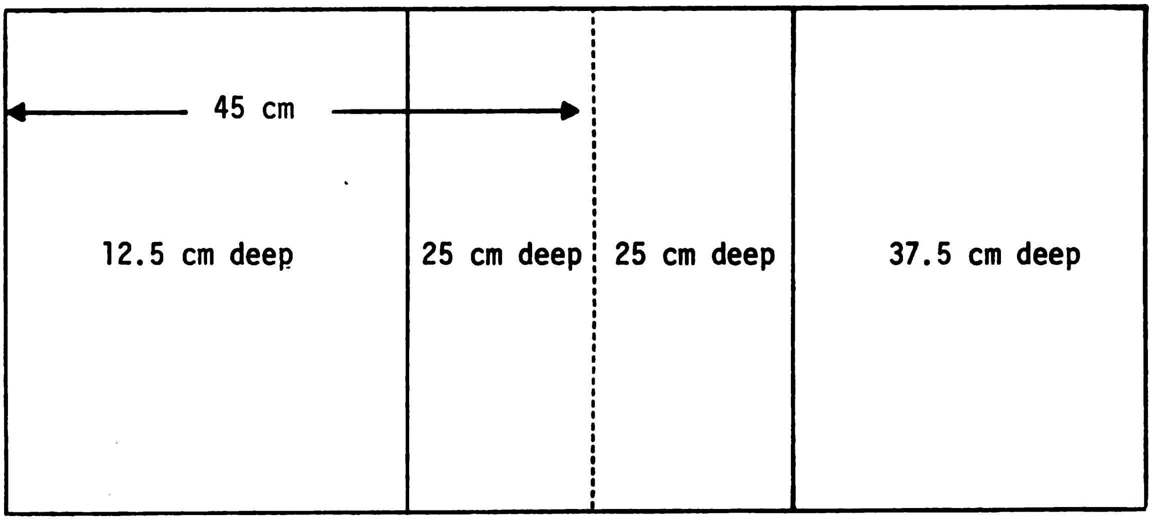
This experiment was set up to examine the effects of light on depth preference in a choice situation. There were three groups of tests. Test I was the same as Group I (DN) in Experiment I where the fish were deep-raised for twelve months and not fed during testing. They were studied in aquaria that were completely lighted. All fish were raised in 37.5 cm. of water until they were a year old. When they were tested they were not fed.

The coded name for the fish in Test I is AL for all light. Test II was done in the same experimental aquaria as Experiment I; however, the shallow half of each aquarium was covered on top with black plastic. This divided the aquarium in half making it necessary to add another dividing line to the experimental aquaria (Figure 4). The darkened half of the aquarium included Areas 1, 2, and 4; the lighted parts were Areas 2.5, 3, 4.5, 5, and 6. This latter half was twice as large a space as the shallow-dark space. This difference was compensated for in the statistical analysis. This compensation was done by dividing the number of times present in the large half of the tanks by two. Test II is coded as SD for shallow dark. The light intensity for Area 1 was .5 lux; Area 4 had a light intensity of 2.0 lux.

Test III, (DD) deep dark, reversed the situation of Test II. This time the black plastic was placed over the deep half of the experimental aquaria. Now Areas 2.5, 3,



SIDE VIEW



TOP VIEW

Figure 4.--Diagram of the experimental tank divided in half for the lighting experiment.

4.5, 5, and 6 were dark and Areas 1, 2, and 4 were light. The light intensity in Area 4.5 was 2.0 lux, and the light intensity in Area 6 was .5 lux.

Fifteen fish were used for each test. The fish were observed for three days after a 24-hour acclimation period.

Statistical Analysis

A significance level of .05 was set *a priori*. Data in Experiment I were analyzed by multivariate and univariate analysis of variance. Further analyses were performed with chi-square independence tests. Comparisons of chi-squares employed the Bonferroni upper percentage points (Dayton and Schafer, 1973) which raised the alpha level required for rejection in accordance with the number of non-independent comparisons made.

RESULTS

Experiment I

Analysis I: Effect of prior experience on 12-month old fish.

Groups I and II (deep-raised, 12-month old fish) were tested against Groups III and IV (shallow-raised, 12-month old fish). A univariate analysis of variance was conducted on Area 1 for each of the three testing days separately. A multivariate analysis of variance was conducted on the other five areas and if the F-ratio for multivariate test of equality of mean vectors was significant at the .05 level for the other areas, then a further guarded F test approach was taken and a univariate analysis of the other five areas was done with reduced alpha levels. Various suggested combinations of areas were also subjected to univariate analyses of variance. The results of these analyses are presented in Table 1. Shallow-raised fish were found significantly more often than deep-raised fish in the shallow, substrate associated Area 1 on day two and day three. Conversely, deep-raised fish were found to be in deep Area 6 more often than shallow-raised fish on day two, and in shallow, open water Area 3 more often on day three. Deep-raised fish were also found significantly more often in open waters (Areas 2, 3, 5) that were not directly associated with a substrate,

Table 1.--Analysis of variance of areas and grouped areas comparing deep-raised 12-month fish to shallow-raised 12-month fish. The fish group that occurs significantly more often is indicated.

Area(s)	Day 1	Day 2	Day 3
1	--	shallow	shallow
2	--	--	--
3	--	--	deep
4	--	--	--
5	--	--	--
6	--	deep	--
1-3	--	--	--
4 & 5	--	--	--
3, 5, 6	--	deep	deep
1, 4, 6	shallow	--	shallow
2, 3, 5	deep	--	deep

whereas shallow-raised fish were found most often associated with areas having a substrate bottom (Areas 1, 4, 6) on days one and three. Deep-raised fish were also found more often in Areas 3, 5, 6 on days two and three; this combination of areas allows for the greatest amount of vertical movement over the shortest distance.

Graphs of the percentages of time spent in the areas that were significant on all three days indicate that the trends were present throughout the testing period (Figures 5 and 6). The one exception to this is Area 6 on day one.

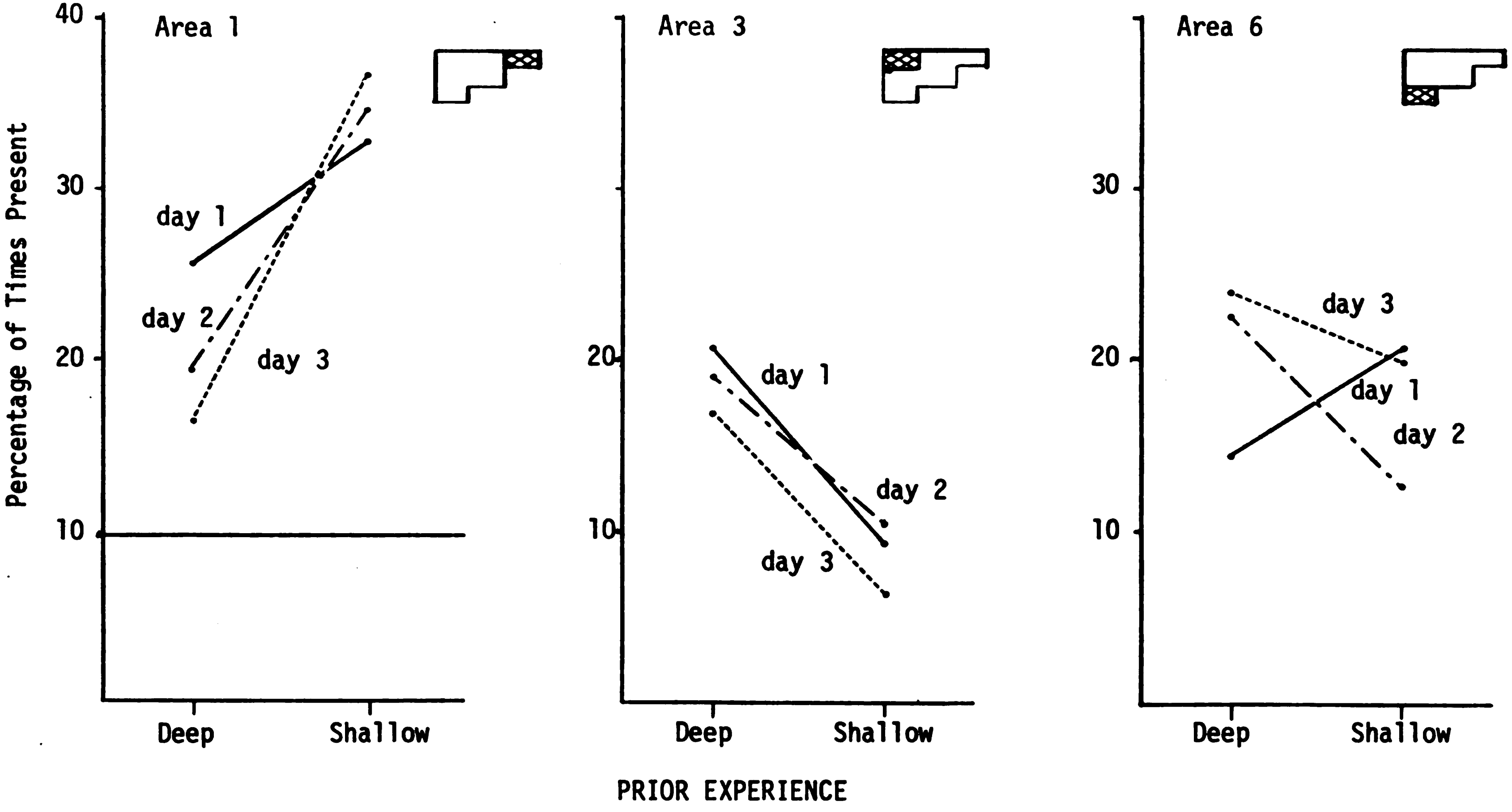


Figure 5.--Graphic presentation of percentage of times present in areas significant in analysis of variance (the other days, though not significant, are also indicated).

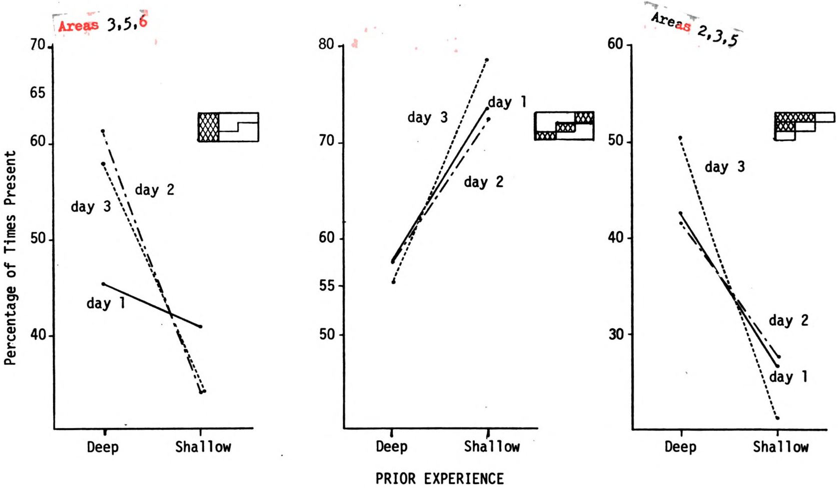


Figure 6.--Graphic presentation of grouped areas that showed significance by analysis of variance (other days, though not significant, are also indicated).

Chi-square analyses of these areas (Table 2) indicate significance of the same days as the analyses of variance. The chi-square also shows that deep-raised fish were present significantly ($p<.005$) more often in Areas 2, 3, 5 on day two, and shallow-raised fish occurred more often in Areas 1, 4, 6 on day two.

Table 2.--Chi-square analyses of some areas comparing deep-raised, 12-month vs. shallow-raised, 12-month. Numbers that were highly significant are indicated by << notation.

Area(s)	Day	Chi-square	Probability	Fish most prevalent
1	1	8.212	<.05	shallow
	2	52.573	<<.005	shallow
	3	90.239	<<.005	shallow
6	1	11.723	<.005	shallow
	2	30.651	<<.005	deep
	3	3.992	n.s.	--
1-3	1	7.391	<.05	deep
	2	5.572	n.s.	--
	3	3.749	n.s.	--
3,5,6	1	9.434	<.01	deep
	2	71.403	<<.005	deep
	3	69.625	<<.005	deep
1,4,6	1	86.374	<<.005	shallow
	2	20.044	<<.005	shallow
	3	49.394	<<.005	shallow
2,3,5	1	70.314	<<.005	deep
	2	37.430	<<.005	deep
	3	100.663	<<.005	deep

Analysis II: Fed vs. Not Fed.

Groups I and III (not fed, 12-month fish) were compared to Groups II and IV (fed, 12-month fish). There were fewer significant results from this analysis of variance of feeding situation than there were from the depth conditioning analysis. Table 3 shows the results. On day one, fed fish occurred more frequently in Area 4; unfed fish occurred more often in Areas 1-3. On day two, fed fish were significantly more often in Area 6; not fed fish were more prevalent in Area 5. There were no significant results on day three.

Table 3.--Analysis of variance of areas and grouped areas comparing fed and not fed fish. The fish group that occurs significantly more often is indicated.

Area(s)	Day 1	Day 2	Day 3
1	--	--	--
2	--	--	--
3	--	--	--
4	fed	--	--
5	--	not fed	--
6	--	fed	--
1-3	not fed	--	--
4 & 5	--	--	--
3, 5, 6	--	--	--
1, 4, 6	--	--	--
2, 3, 5	--	--	--

Graphs (Figure 7) of some percentages indicate certain trends. Unfed fish were in the grouped shallow water areas

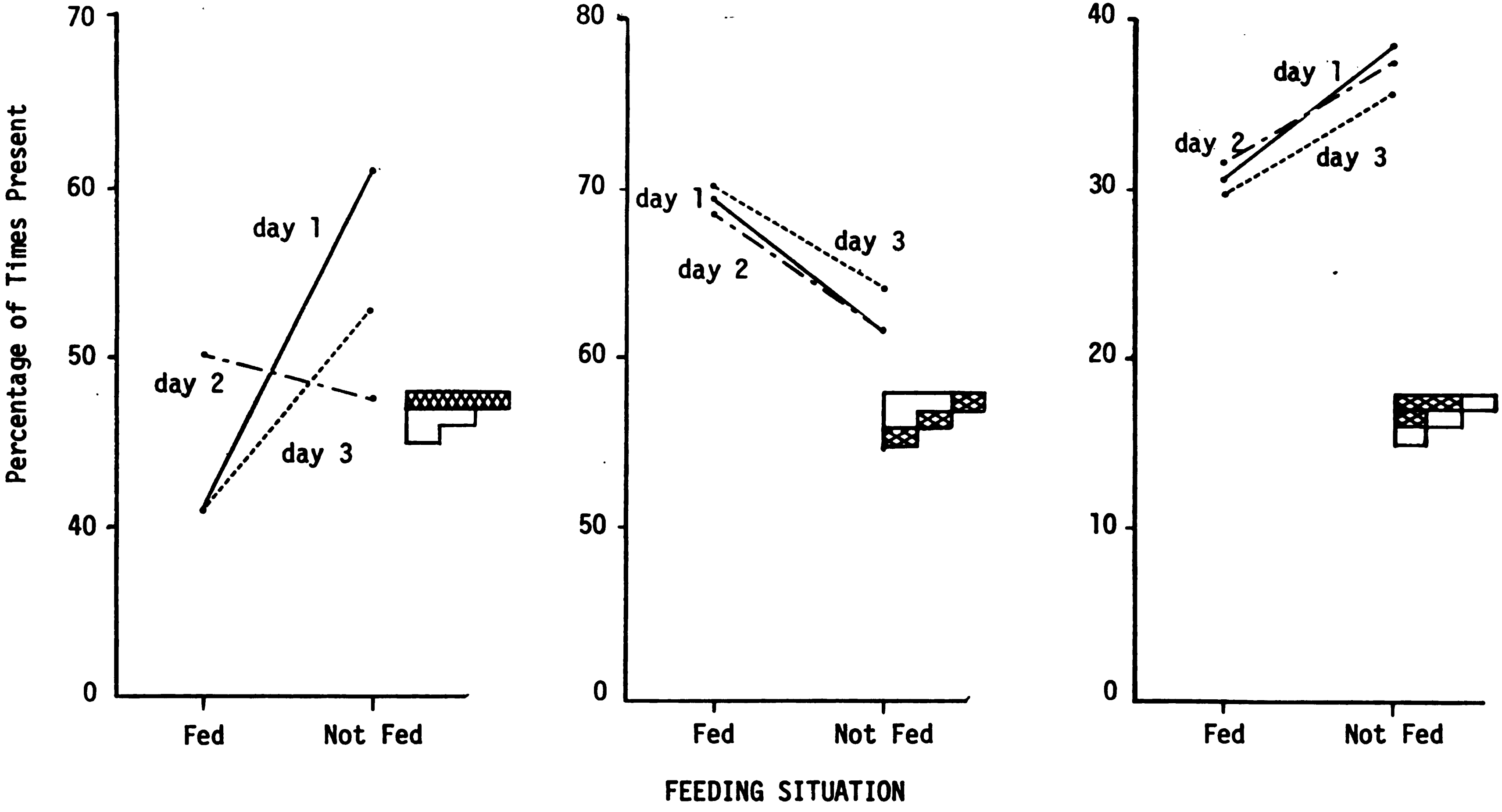


Figure 7.--Graphic presentation of percentage of times present in areas comparing fed with not fed fish.

of 1-3 more often on two days out of three whereas fed fish were in grouped Areas 1, 4, 6 more often on all three days. Conversely, not fed fish were in open water Areas 2, 3, 5 more often than fed ones.

A set of chi-square analyses (Table 4) shows results for only days two and three because the fish would probably show greater differences than on day one. This is because on day one the unfed fish would probably not be hungry enough to show much difference in behavior. Again fed fish are more associated with the substrata in Area 6 on both days and Area 4 on day three. Unfed fish were in Area 1, and Areas 1-3 by day three and in Areas 2, 3, 5 on day two.

Table 4.--Chi-square analyses of some areas comparing fed vs. not fed fish.

Area(s)	Day	Chi-square	Probability	Fish Most prevalent
1	2	0.394	n.s.	--
	3	16.115	<.005	not fed
4	2	0.739	n.s.	--
	3	10.629	<.005	fed
6	2	15.094	<.005	fed
	3	20.408	<<.005	fed
1-3	2	0.373	n.s.	--
	3	18.145	<.005	not fed
2,3,5	2	8.231	<.01	not fed
	3	6.562	n.s.	--

Analysis III: Interactions between experience and feeding situation.

Analyses of variance were carried out as before in Analyses I and II to determine the effects of any interactions that may have occurred between the early experience of a fish and its feeding situation (Table 5). Interactions occurred in Area 1 and Areas 3, 5, 6 on day two and in Area 6 on days one and two. There were also interactions in Areas 2, 3, 5 on days one and two and in Areas 1, 4, 6 on all three days.

Table 5.--Analysis of variance of interaction between early experience and feeding situation.

Area(s)	Day 1	Day 2	Day 3
1	--	interaction	--
2	--	--	--
3	--	--	--
4	--	--	--
5	--	--	--
6	interaction	interaction	--
1-3	--	--	--
4 & 5	--	--	--
3, 5, 6	--	interaction	--
1, 4, 6	interaction	interaction	interaction
2, 3, 5	interaction	interaction	--

Figures 8, 9 and 10 show the direction of these interactions. There is a disordinal interaction in Area 1 on day two. The unfed fish were unaffected by prior experience whereas fed fish were influenced by both shallow and deep rearing conditions. Interestingly, these effects were the reverse of each other with deep-raised fed fish avoiding Area 1 and shallow-raised fed fish being most prevalent. Area 6 showed interactions on both day one and day two. On day one shallow-raised fish were affected by feeding conditions; deep-raised fish were little influenced. By day two experience and feeding situations all interacted.

Graphs of combined areas (Figure 9) also show interactions. Areas 3, 5, 6 day two, indicate definite effects of all parameters. Deep-raised fish were present more often than shallow-raised fish. Again there is a reversal between deep-raised and shallow-raised fish with deep-raised fed fish being in Areas 3, 5, 6 most often and shallow-raised fed fish being there least often. Both day one and day two of Areas 2, 3, 5 show the same interaction. Not fed fish were little influenced by experience but fed fish showed an interaction with both rearing conditions. Deep-raised fish were present in Areas 2, 3, 5 most often when they were fed; shallow-raised fish were there least often when fed.

Areas 1, 4, 6 (Figure 10) showed a changing interaction over time. On days one and two there was only a slight effect of not feeding on both prior experience groups. The fed fish

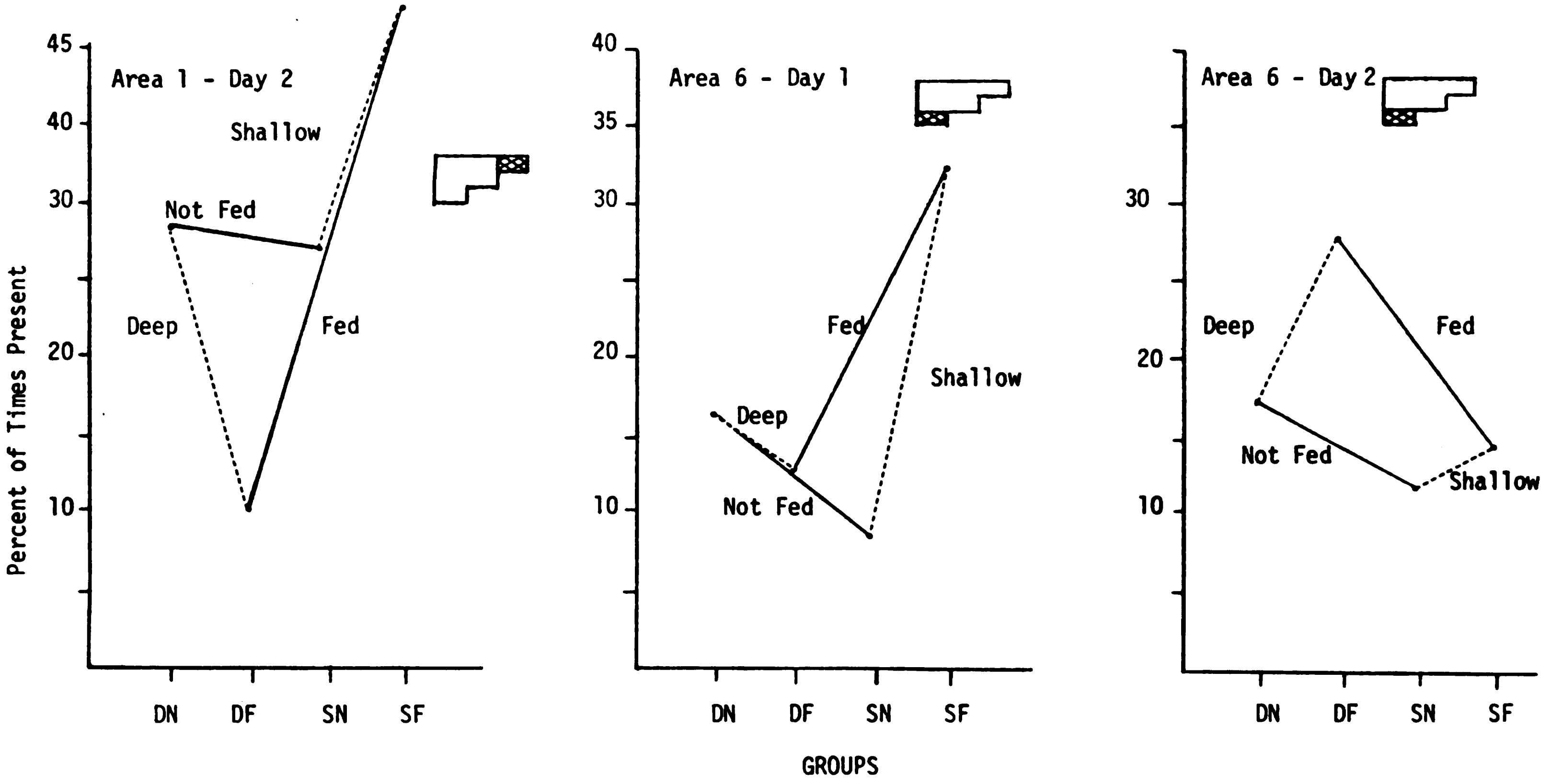


Figure 8.--Percentage of times present in groups graphed to show interactions of Area 1, day 2 and Area 6, day 1 and day 2.

Legend explaining abbreviations:
DN = Deep-raised, not fed
DF = Deep-raised, fed
SN = Shallow-raised, not fed
SF = Shallow-raised, fed

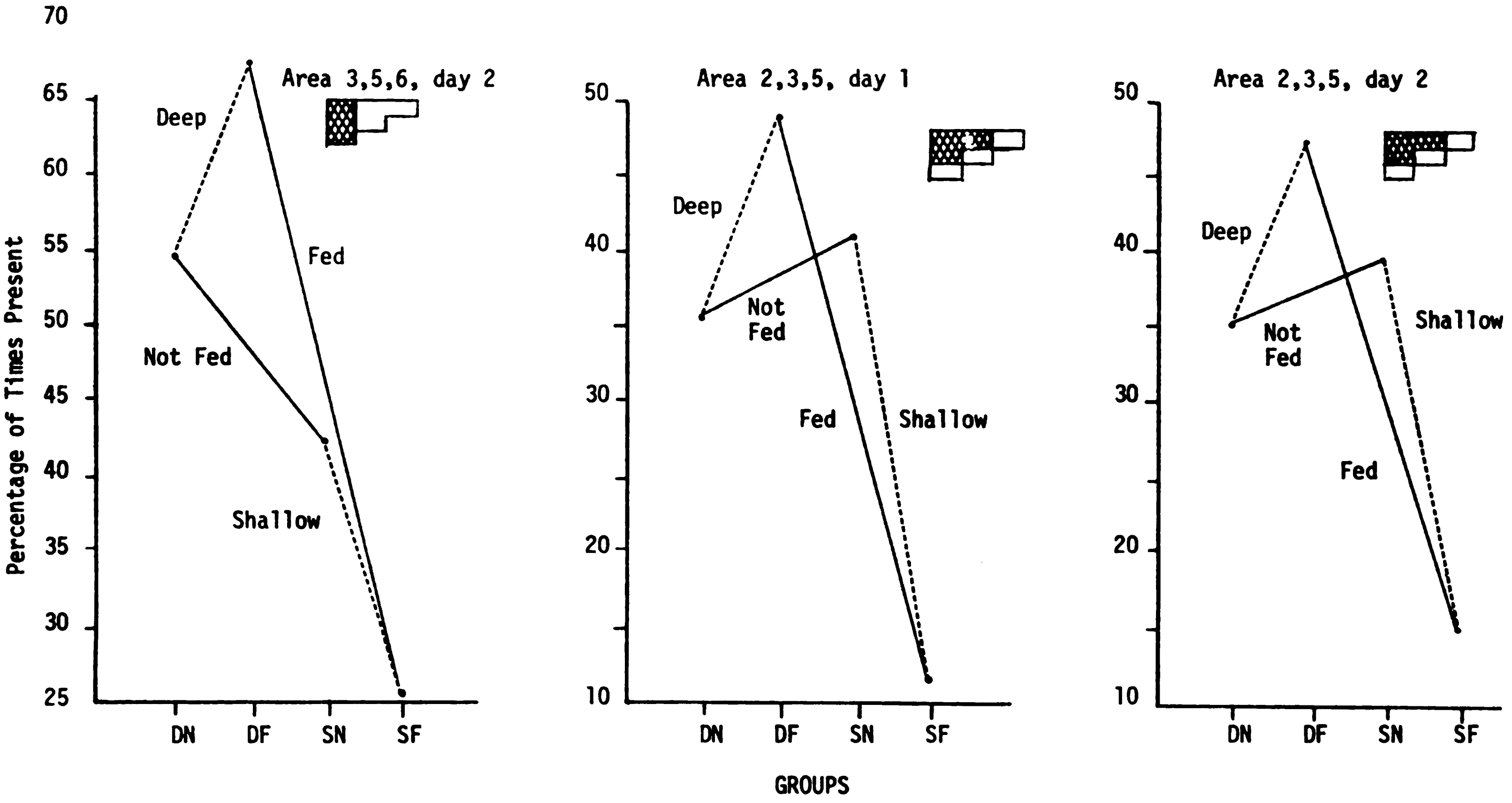


Figure 9.--Percent of times present in Areas 3,5,6, day 2 and Areas 2,3,5, day 1 and day 2 to show interactions.

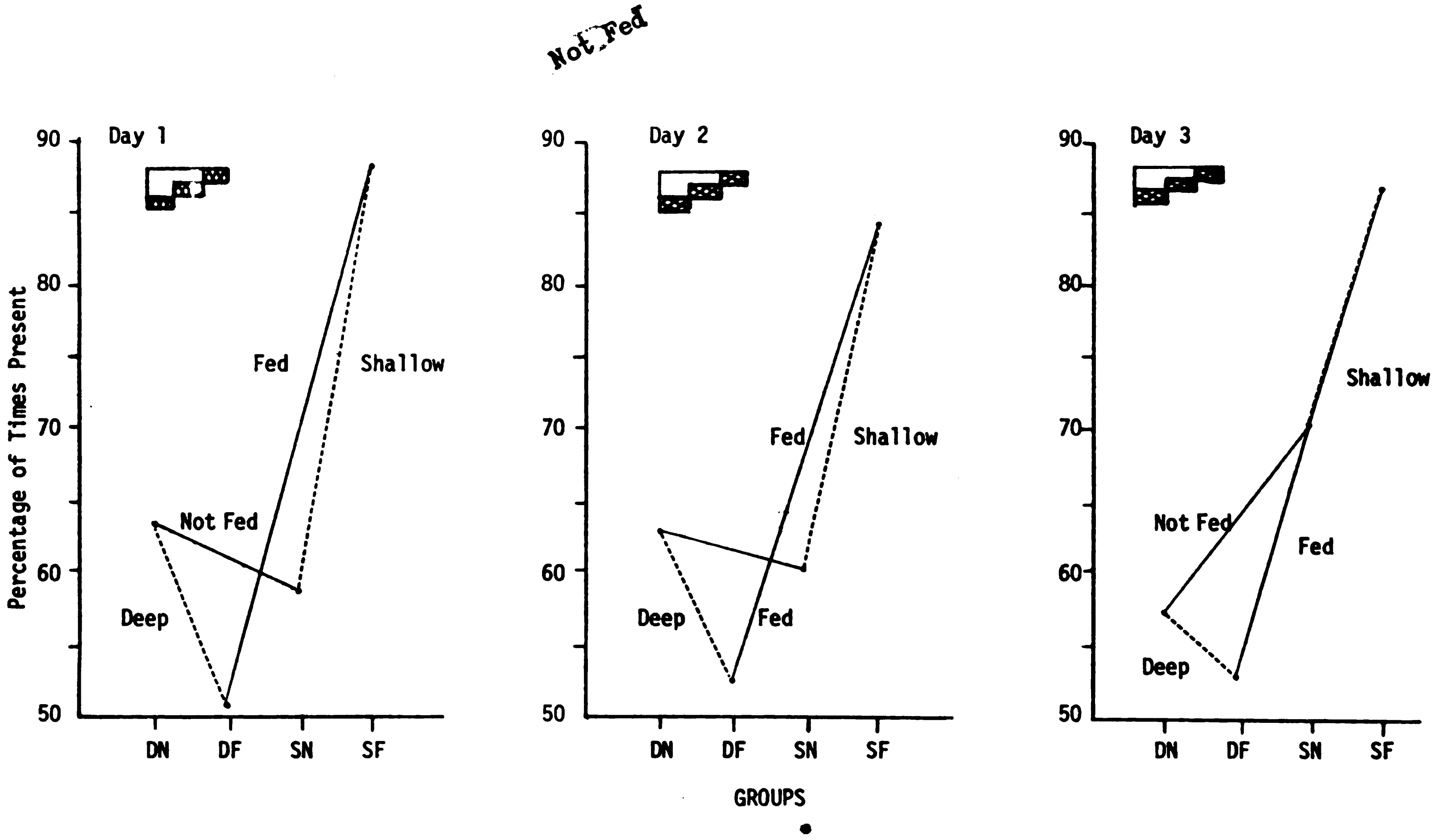


Figure 10.--Percent of times present in Areas 1,4,6 graphed to show interactions.

that were shallow-raised were present much more often than any other group. The fed deep-raised fish were present the least amount of time. By day three the shallow-raised fish were always present more often than deep-raised fish. Once again shallow-raised fed fish were there most often; deep-raised fed fish were there least often.

Behavior Analysis

Table 6 presents the results of a record of the activities of the fish. Part I shows all groups listed separately and the number of swim bouts occurring each day. The most active group was deep-raised not fed (DN) fish; the least active were shallow-raised fed (SF) fish. When deep-raised fish were compared with shallow-raised fish (Part II) the not fed fish were much more active.

Parts IV-VI present the results of the numbers of feeding movements made by each group. In Part IV the group feeding most is SF fish; DN fish made the fewest feeding movements. Shallow-raised fish (Part V) made many more feeding movements than deep-raised fish. In Part VI fed fish usually made more feeding movements than unfed fish. The exception to this is day one where the number of feeding movements is about equal.

Analysis IV: Comparison of 6-month fish to 12-month fish.

Groups I and III (12-month old, not fed fish) were compared to Groups V and VI (6-month old, not fed fish). The

Table 6.--Results of activity counts of swim bouts and feeding movements. DN = deep-raised, not fed fish; DF = deep-raised, fed fish; SN = shallow-raised, not fed fish; SF = shallow-raised, fed fish.

Part I. All groups to show swim bouts.

Group	Day One	Day Two	Day Three
DN	133	185	221
DF	106	50	146
SN	58	110	77
SF	40	4	0

Part II. Number of swim bouts of deep-raised and shallow-raised fish.

Group	Day One	Day Two	Day Three
Deep-raised	239	235	367
Shallow-raised	98	114	77

Part III. Number of swim bouts of fed and not fed fish.

Group	Day One	Day Two	Day Three
Fed Fish	146	54	146
Not Fed Fish	191	295	298

Part IV. All groups to show feeding movements.

Group	Day One	Day Two	Day Three
DN	113	20	38
DF	55	158	80
SN	75	51	178
SF	196	156	224

Part V. Number of feeding movements of deep-raised and shallow-raised fish.

Group	Day One	Day Two	Day Three
Deep-raised	168	178	118
Shallow-raised	271	207	402

Part VI. Number of feeding movements of fed and not fed fish.

Group	Day One	Day Two	Day Three
Fed Fish	251	314	304
Not Fed Fish	288	71	216

analysis of variance (Table 7) showed that 6-month fish were found significantly more often in Area 4 on days one and three, whereas 12-month fish were in Area 5 significantly more often on day two. In the analysis of the grouped areas 6-month fish were in mid-water Areas 4 and 5 more often on days one and three; they were in Areas 1, 4, 6 more often on days one and two. Twelve-month fish were in the shallow water region, Areas 1-3, more often on day one and day three and in the open water region (Areas 2, 3, 5) more often on days one and two. Graphs of some significant grouped areas on other days (Figure 11) indicate that the same trends are present.

Table 7.--Univariate analysis of variance of 6-month fish compared to 12-month fish. The age group that occurs significantly more often is indicated.

Area(s)	Day 1	Day 2	Day 3
1	--	--	--
2	--	--	--
3	--	--	--
4	6-month	--	6-month
5	--	12-month	--
6	--	--	--
1-3	12-month	--	12-month
4 & 5	6-month	--	6-month
3, 5, 6	--	--	--
1, 4, 6	6-month	6-month	--
2, 3, 5	12-month	12-month	--

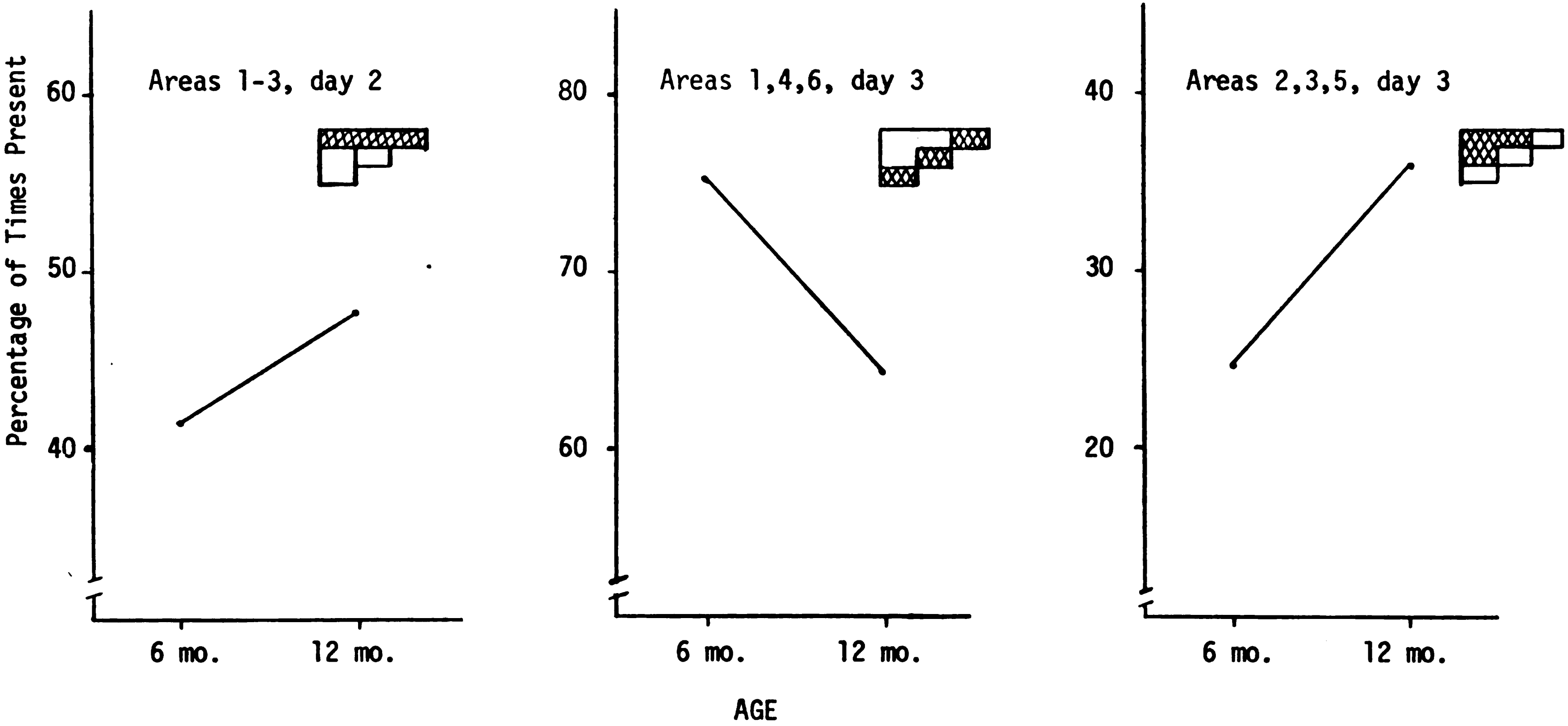


Figure 11.--Percent of times present in some areas comparing 6 month to 12 month fish.

Table 8 shows the results of some chi-square analyses. Area 4 shows the dominance of 6-month fish on every day. Areas 1, 4, 6 also have 6-month fish present every day at a highly significant level. Twelve-month fish are found in Areas 1-3 and 2, 3, 5 significantly more often than 6-month fish on all three days.

Table 8.--Chi-square analyses of 6-month fish vs. 12-month fish.

Area(s)	Day	Chi-square	Probability	Fish Most Prevalent
4	1	72.471	<<.005	6-month
	2	28.167	<<.005	6-month
	3	71.505	<<.005	6-month
1-3	1	75.792	<<.005	12-month
	2	6.545	<.01	12-month
	3	35.769	<<.005	12-month
1,4,6	1	24.288	<<.005	6-month
	2	16.746	<.005	6-month
	3	10.888	<.005	6-month
2,3,5	1	56.672	<<.005	12-month
	2	36.546	<<.005	12-month
	3	25.036	<<.005	12-month

Analysis V: Analysis for differences in experience of 6-month and 12-month fish.

Groups I and V (deep-raised fish) and Groups III and VI (shallow-raised fish) were compared. The age differences were not considered in this analysis. The same procedure as in all preceding analyses was followed with the analysis of variance. Table 9 shows shallow-raised fish present in Area 4

Table 9.--Analysis of variance of all deep-raised fish compared to all shallow-raised fish. The group that occurs significantly more often is indicated.

Area(s)	Day 1	Day 2	Day 3
1	--	--	--
2	--	--	--
3	--	--	--
4	--	shallow	shallow
5	--	--	deep
6	--	--	--
1-3	--	--	--
4 & 5	--	--	--
3, 5, 6	--	deep	deep
1, 4, 6	shallow	shallow	shallow
2, 3, 5	deep	deep	deep

more often than deep-raised fish on days two and three and in Areas 1, 4, 6 more often every day. Deep-raised fish were in Area 5 more often on the third day. In grouped areas deep-raised fish were in open water regions (Areas 2, 3, 5) more frequently than shallow-raised fish on all three days, and they were in Areas 3, 5, 6 more often on the second and third day. Figure 12 shows that these results are also similar on the other days but at a lower level of significance.

Chi-square results, Table 10, show that shallow-raised fish were in Area 4 and Areas 1, 4, 6 at a highly significant level every day. At an equally high significance,

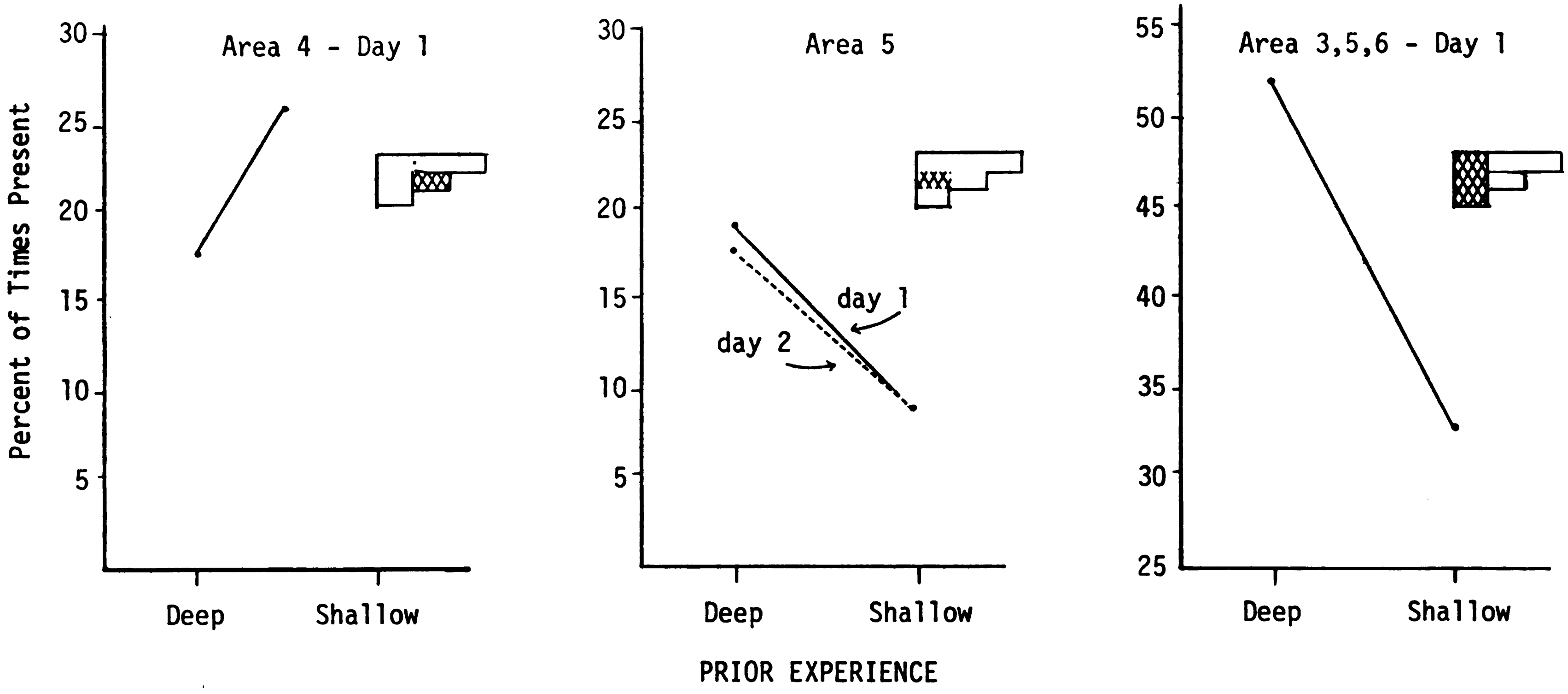


Figure 12.--Trends indicated by graphs of percent of times present in Area 4, Area 5, and Areas 3,5,6.

Table 10.--Chi-square analysis of 6-month plus 12-month fish comparing deep and shallow raising.

Area(s)	Day	Chi-square	Probability	Fish Most Prevalent
4	1	18.307	<.005	shallow
	2	89.707	<<.005	shallow
	3	62.027	<<.005	shallow
5	1	23.121	<<.005	deep
	2	33.156	<<.005	deep
	3	61.075	<<.005	deep
3,5,6	1	69.778	<<.005	deep
	2	47.127	<<.005	deep
	3	64.157	<<.005	deep
1,4,6	1	16.402	<.005	shallow
	2	17.973	<.005	shallow
	3	21.339	<<.005	shallow
2,3,5	1	38.272	<.005	deep
	2	36.236	<.005	deep
	3	24.794	<.005	deep

deep-raised individuals were present in Area 5, Areas 3, 5, 6 and Areas 2, 3, 5 all days tested.

Analysis VI: The interaction of age and experience.

Table 11 shows the results of the analysis of variance. There were few interactions. Areas 1-3, and Areas 4 and 5 indicate interactions on day three. Areas 1, 4, 6 and 2, 3, 5 on day one and day two have interactions indicated. Graphs (Figures 13 and 14) indicate the direction of the interactions. In Areas 1-3 and Areas 4 and 5, deep-raised fish were unaffected by age whereas shallow-raised fish were very much influenced by age. Six-month shallow-raised fish were in Areas 4 & 5

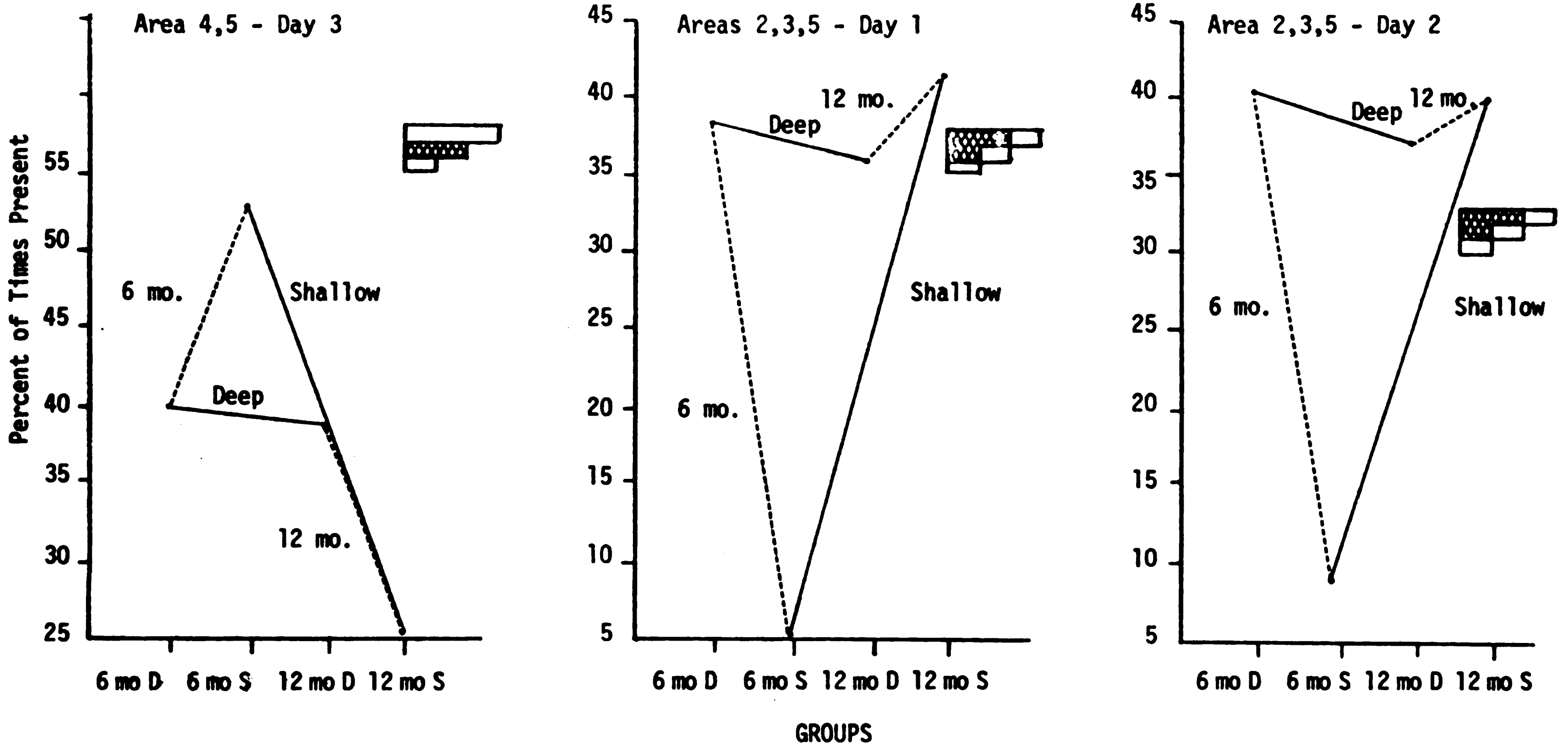


Figure 13.--Percent of times present in Areas 4 and 5 and Areas 2,3,5 to show interactions.

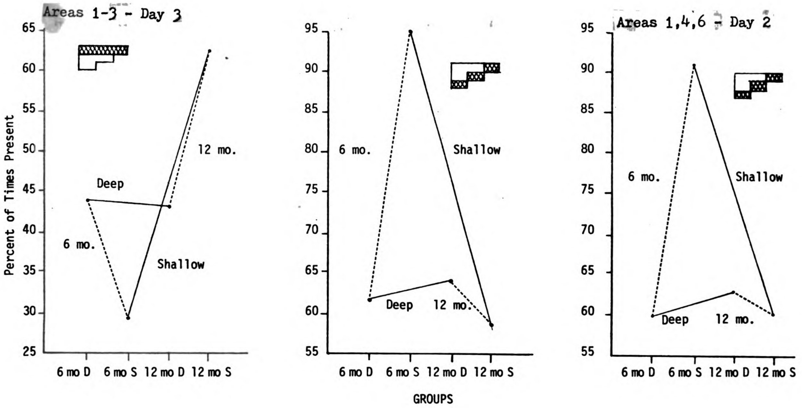


Figure 14.--Percent of times present in Areas 1-3 and Areas 1,4,6 graphed to show interactions.

Table 11.--Analysis of variance of the interaction of age and experience.

Area(s)	Day 1	Day 2	Day 3
1	--	--	--
2	--	--	--
3	--	--	--
4	--	--	--
5	--	--	--
6	--	--	--
1-3	--	--	interaction
4 & 5	--	--	interaction
3,5,6	--	--	--
1,4,6	interaction	interaction	--
2,3,5	interaction	interaction	

most often of all groups; they were in Areas 1-3 least often of all groups. Conversely, 12-month shallow-raised fish were in Areas 4 & 5 least often and in Areas 1-3 most often. Areas 1, 4, 6 display the combined effect of shallow-raising and age. There is little influence of age on deep-raised fish. Shallow-raised 6-month fish occurred in Areas 1, 4, 6 much more often than any other groups; shallow-raised 12-month individuals are present the most infrequently. The graphs of Areas 2, 3, 5 are simply inverted graphs of Areas 1, 4, 6 and therefore show the opposite effects.

Experiment II

Twelve-month old unfed fish were tested under three lighting conditions: an all-light aquarium, a shallow-dark aquarium, and a deep-dark aquarium (See materials and methods section for a detailed description). Figure 15 graphs the percentages of time present of fish tested under all light conditions (AL), shallow-dark (SD), and deep-dark (DD) conditions in Areas 1-3; 1, 2, 4; and the other half of the aquarium (Areas 2.5, 3, 4.5, 5, 6). The graph of Areas 1-3 (all shallow) show that SD tested fish were usually present least often. Similarly, the percentages for Areas 1, 2, 4 indicate the SD fish are also avoiding those areas. In the other half of the experimental aquaria (Areas 2.5, 3, 4.5, 5, 6) SD fish were present considerably more often than AL or DD fish (under shallow-dark conditions these areas were darkened). Table 12 lists some other percentages of time present of selected groups of areas. Most of the percentages support the idea that SD tested fish avoided all the shallow areas of the aquaria especially the darkened ones.

Table 13 presents a chi-square analysis of certain areas comparing AL fish with SD fish. AL fish were present in Areas 1, 2, 4 to a highly significant degree compared with SD fish. SD fish were in Area 6 more often every day and in the remaining areas more often on days one and two.

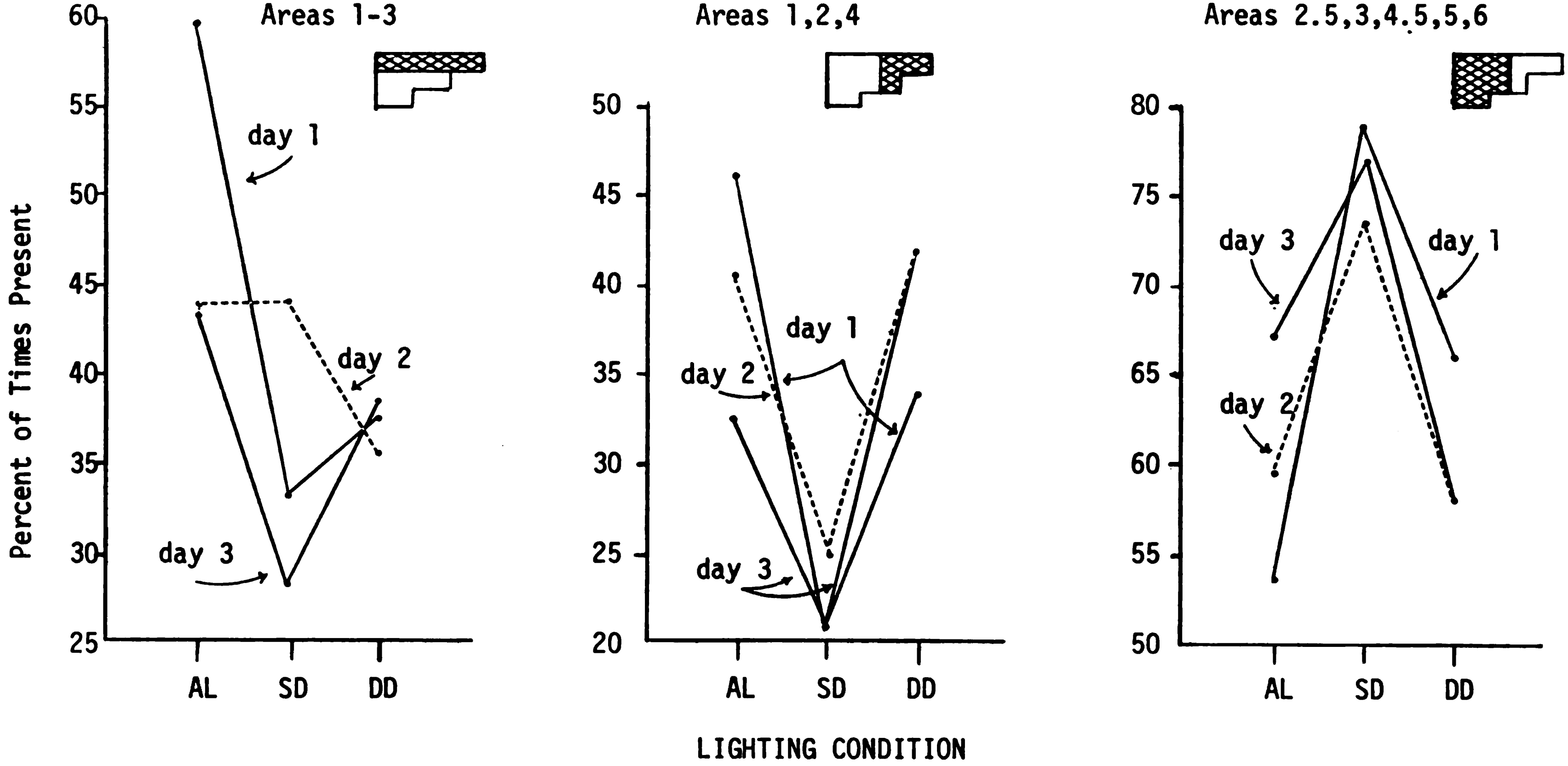


Figure 15.--Graphic presentation of percent of times present in Areas 1-3, Areas 1,2,4 and Areas 2.5,3,4.5,5,6.

Table 12.--Percentage of times present of some grouped areas comparing all-lit, shallow-dark and deep-dark tested fish.

Area(s)	Day	AL	SD	DD
3,5,6	1	44.0	67.8	54.3
	2	45.7	59.2	48.3
	3	55.8	68.8	50.5
1&2	1	40.5	16.2	27.8
	2	31.9	22.0	27.8
	3	30.0	16.5	31.8
2.5&3	1	19.2	17.2	9.7
	2	11.7	22.0	7.7
	3	21.1	11.8	6.7
4.5&5	1	18.5	33.0	24.7
	2	28.8	21.5	19.3
	3	27.0	24.8	14.0
2&4	1	9.8	6.2	14.2
	2	12.0	9.5	21.0
	3	15.5	5.5	16.5
2.5&4.5	1	9.8	11.2	11.7
	2	12.0	14.8	13.8
	3	15.5	10.0	7.5
2, 2.5, 4, 4.5	1	19.5	17.4	25.8
	2	24.0	24.3	34.8
	3	31.0	15.5	24.0

Table 13.--Chi-square comparison of AL vs. SD fish.

Area(s)	Day	Chi-square	Probability	Fish Most Prevalent
1	1	54.870	<<.005	AL
	2	18.601	<.005	AL
	3	4.928	n.s.	--
6	1	173.556	<<.005	SD
	2	21.898	<<.005	SD
	3	33.153	<<.005	SD
1,2,4	1	237.047	<<.005	AL
	2	18.682	<.005	AL
	3	14.740	<.005	AL
2.5,3,4.5 5,6	1	28.816	<.005	SD
	2	9.359	<.01	SD
	3	5.429	n.s.	--

In Table 14 a chi-square analysis of DD versus AL fish was conducted. All light fish were shown to appear more often in the shallow waters (Area 1, Area 3, Areas 1-3) whereas DD fish occurred more often in Area 6.

Table 14.--Chi-square comparison of DD vs. AL fish.

Area(s)	Day	Chi-square	Probability	Fish Most Prevalent
1	1	29.586	<<.005	AL
	2	18.015	<.005	AL
	3	1.076	n.s.	--
3	1	25.992	<<.005	AL
	2	27.000	<<.005	AL
	3	32.529	<<.005	AL
6	1	29.389	<<.005	DD
	2	37.146	<<.005	DD
	3	19.904	<.005	DD
1-3	1	122.278	<<.005	AL
	2	7.177	<.05	AL
	3	1.713	n.s.	--

Next (Table 15) a comparison of SD and DD fish was performed. There were no significant differences between SD and DD fish in Area 6 and little difference in their responses to Areas 1-3. However DD fish were present more often on all days in Areas 1, 2, 4 which is the shallow water region (this region was lit for DD fish and dark for SD fish).

Table 15.--Chi-square comparison of DD vs. SD fish.

Area	Day	Chi-square	Probability	Fish Most Prevalent
6	1	0.796	n.s.	--
	2	2.140	n.s.	--
	3	1.763	n.s.	--
1-3	1	6.259	<.05	DD
	2	5.453	n.s.	--
	3	9.279	<.01	DD
1,2,4	1	9.529	<.01	DD
	2	12.760	<.005	DD
	3	20.506	<<.005	DD
2.5, 3, 4.5,5,6	1	3.262	n.s.	--
	2	6.005	n.s.	--
	3	7.983	<.05	SD

Some areas within each experiment were tested against each other. Table 16 shows the chi-square analyses of areas tested under shallow-dark conditions. The lit areas of the aquaria were always preferred to the shallow-darkened areas. Area 6 was preferred to both Area 1 and Area 3. The areas that were near the light-dark boundary, Areas 2.0, 2.5, 4.0, 4.5 were avoided.

Table 17 compares areas of deep-dark testing. Again Area 6 was preferred to both Area 1 and Area 3. Areas 1, 2, 4 were not selected to any greater extent than the other areas. The two shallowest lighted areas (Areas 1 and 2) are preferred to the two shallowest darkened areas (2.5 and 3). The light-dark boundary (Areas 2.0, 2.5, 4.0, 4.5) is also avoided.

Table 16.--Chi-square analyses of areas in shallow-dark testing.

	Day	Chi-square	Probability	Areas Preferred
Areas 1,2,4 vs. remaining areas (2.5,3,4.5,5,6)	1	33.942	<<.005	2.5,3,4.5,5,6
	2	10.991	<.005	2.5,3,4.5,5,6
	3	32.990	<<.005	2.5,3,4.5,5,6
Areas 1-3 vs. 4-6	1	66.666	<<.005	4-6
	2	8.640	n.s.	---
	3	112.666	<<.005	4-6
Area 1 vs 6	1	26.931	<<.005	6
	2	23.844	<<.005	6
	3	9.626	<.01	6
Area 3 vs. 6	1	24.060	<<.005	6
	2	20.658	<<.005	6
	3	125.759	<<.005	6
Areas 2,2.5,4, 4.5 vs. Remaining Areas	1	256.107	<<.005	Remaining Areas
	2	158.107	<<.005	Remaining Areas
	3	285.660	<<.005	Remaining Areas

Table 17.--Chi-square analyses of areas in deep-dark testing.

	Day	Chi-square	Probability	Areas Preferred
Area 1 vs. 6	1	16.313	<.005	6
	2	38.782	<<.005	6
	3	38.116	<<.005	6
Area 3 vs. 6	1	108.649	<<.005	6
	2	169.982	<<.005	6
	3	172.942	<<.005	6
Areas 1,2,4 vs. 2.5,3,4.5,5,6	1	2.308	n.s.	---
	2	3.963	n.s.	---
	3	0.555	n.s.	---
Areas 2,2.5,4, 4.5 vs. Remaining Areas	1	121.500	<<.005	Remaining Areas
	2	55.207	<<.005	Remaining Areas
	3	86.640	<<.005	Remaining Areas
Areas 1 & 2 vs. 2.5 & 3	1	52.804	<<.005	1 & 2
	2	68.737	<<.005	1 & 2
	3	98.706	<<.005	1 & 2

DISCUSSION

Experiment I

One result of this experiment indicates that prior experience is important in establishing a fish's depth utilization. In this study prior experience at a given depth played a significant role in the depth preference of Haplochromis burtoni. The first analysis showed that shallow-raised, 12-month old fish preferred shallow water area 1 (every day) and also areas that were directly associated with a substrate (areas 1, 4, 6). Perhaps the close association with the substrate indicates a tendency for the shallow-raised fish to remain in protected areas. Shallow-raised fish had not previously experienced deep water or shallow water that was not directly associated with substrate, so therefore, these areas represented unfamiliar environmental conditions to be avoided. The conclusions are supported by the behavioral data which indicated that shallow-raised fish did not make as many swim bouts as deep-raised individuals. The lack of activity by shallow-raised fish could be considered a fear response. A frightened fish will seek cover and if the only cover available is a substrate, the fish may lie near the bottom. When Haines and Butler (1969) offered smallmouth bass only a dark-colored bottom plate for shelter, the bass utilized it. Similarily, Ritter and MacCrimmon (1973) found that rainbow trout would remain close to a black colored bottom as if it offered some type of protection. These trout are dorsally dark and ventrally light so a dark bottom could indeed represent cover. Remaining close to the bottom is not the only fear response a fish may give; it may freeze or cower in the upper corner of an aquarium as a subordinate fish will often do when confronted by a more dominant fish.

The reactions of the fish may include both avoidance and exploratory behavior which has been related to fear induced by novel stimuli (Montgomery, 1955 and Russell, 1967). Montgomery found that when novel stimuli were presented to an animal, they evoked both avoidance and exploration. Kleerekoper et al. (1974) showed that goldfish would systematically avoid, then explore, areas of an aquarium in a specific way. The presence of shallow-raised fish in area 4 might indicate mild exploratory behavior of an area that was partially familiar, while the fish's absence in most open waters and area 6 might indicate avoidance of a less familiar region.

Analysis 1 also showed that deep-raised, 12-month old fish preferred area 6 and grouped areas 2, 3, 5; 3, 5, 6 and 1-3 (on day one). This indicates that they utilize the open waters of the experimental aquaria and also range over wide spaces. On a vertical plane the longest distance a fish can swim is from area 3 to area 6. Horizontally the longest distance is from area 1 to area 3. These are the areas where deep-raised fish occurred significantly more often than shallow-raised fish. The fact that deep-raised fish were in areas 1-3 on day one more often than shallow-raised fish seems inconsistant with the fact that shallow-raised fish were in area 1. However, if deep-raised fish were ranging from area 1 to area 3, and because they were found more often in area 3, they would appear to be present in the grouped areas much more often than shallow-raised fish that were only in area 1. Deep-raised fish would have already experienced the vertical and horizontal distances present in the experimental tanks and therefore, the distances would not be novel stimuli to be avoided. Also, if deep-raised fish were considered experienced, and shallow-raised fish were considered deprived then according to Sale (1969a.) the activity level of the two groups should be different. However, Sale would have predicted opposite results. His hypothesized mechanism of habitat selection predicts that activity levels should be greater in a preferred habitat. The preferred habitat he used was shallow water with cover which is where the juvenile manini are found. The inadequate habitat was deep water with no cover. I considered, as did Sale, swim bouts to be measures of exploration and feeding movements to be non-exploratory activities. My results showed that fish in a more familiar habitat (deep-raised fish) were more active (exploratory) and showed fewer non-exploratory activities (feeding movements). Fish in a less familiar habitat (shallow-raised fish) were less exploratory and made more feeding movements. These results do not concur with Sale's hypothesis. This may be due to some differences in our experiments. I used a different species. The fish in the experiment had the ability to choose areas of the aquarium that were most like the ones they had previously encountered whereas Sale's test gave them only one habitat type at a time. Sale's observations were made only one hour after the fish was placed into a new habitat, and after the observation it was placed into another habitat and again observed. I do not feel that this is adequate time for a fish to show any definitive behavior other than a fear response.

When fed, 12-month old fish were compared to unfed, 12-month old fish the results were similar to the comparison of shallow-raised fish with deep-raised fish. The fed fish, like shallow-raised fish, were associated with areas directly adjacent to the substrate, areas 1, 4, 6. The difference between shallow-raised and fed fish is in area 6. Fed fish were in area 6 significantly more often than unfed fish, whereas deep-raised fish were in area 6 more often than shallow-raised fish. This difference is accountable if one considers that the fed fish were feeding off the bottom surfaces of the aquaria and would therefore be in every substrate associated area including area 6. Woodhead (1964) noted that changes in vertical distribution are associated with feeding, and hungry minnows were not limited by their usual light-temperature optima when they were hungry. Brunel (1964) stated that cod, which are usually nocturnal, will move off the bottom during the day if food is present. Therefore it is reasonable to expect that the Haplochromis burtoni would utilize all depths of the aquaria. Welcomme (1964) observed that Haplochromis are generalized bottom feeders, and therefore they would be feeding off the bottom surface areas. When prior experience is considered, shallow-raised fish were probably avoiding area 6 because it had an unfamiliar depth. As for the presence of shallow-raised fish and the absence of fed fish in area 3, it appears that fed fish were feeding off the substrate associated areas and would therefore avoid the open water areas. Shallow-raised fish would be more likely to be in area 3 because that area is a shallow water area and partially familiar to them.

When the fish were fed, the food flakes were sprinkled evenly across the top surface areas. After the flakes became moist they sank to the substrate. Unfed fish were more active than fed fish and were present in open areas more often. If these unfed fish were searching for food, one would expect them to spend a considerable amount of time patrolling the top surface of the water (areas 1-3), because this was where the food was first encountered. This was indeed the case. Unfed fish were present in areas 1-3 more often than fed fish on day one and day three. As for day two, perhaps the fed fish were still hungry after being fed on day two or perhaps they were less stressed for food and were exploring areas 1-3 on that day.

Montgomery (1953) indicated that food deprivation reduces the amount of investigation because a more primary drive, food seeking, replaces it. The unfed fish in Experiment I spent more time actively searching for food than passively exploring the features of the aquarium. This is shown by the larger amount of time they spent performing swim bouts.

There is considerable argument concerning the mechanism involved with food deprivation and exploration. Alderstein and Feherer (1955) believe that hunger lowers the threshold of responsiveness to the environment. They found that hungry animals explore more and at a more constant rate than satiated ones, and that this exploration decreases with time. This finding would be reflected by the fact that the unfed fish were more active than the fed ones. This activity, however, increased instead of decreased with time. Campbell and Sheffield (1953) state that the hunger drive does not force activity; it merely makes the animal more responsive to environmental changes. They believe that if the environment does not change there will be little increase in activity. My results do not agree with this. Although the experimental aquaria were not changed, the activity of the hungry fish increased.

I believe the lack of concensus among scientists studying deprivation and exploration depends on their interpretation of exploratory behavior. Some activities that are directly related to food seeking can be called exploratory behavior; others cannot. For example: a hungry _Haplochromis burtoni_ will actively investigate any object floating on the top surface of its aquarium but will spend little to no time exploring an object on the bottom of the tank (personal observation). I have used this behavior often when I wanted to introduce a new fish into a group. If I introduced the fish into a tank of hungry fish, they were not as likely to notice the fish as much as fed fish would. As long as the hungry fish were not starved, and therefore highly aggressive, they accepted the new fish without injury.

When the interactions of depth conditioning and feeding situation were studied it was possible to establish a hierarchy of importance. Hungry fish were little influenced by prior experience. A fish that was deprived of food had a major interest in food seeking and, therefore, prior experience was secondary. Barnett (1958) found that activity decreased with time in an environment but this decrease only occurred when there was not a higher pressure, such as hunger, influencing the animal. Unfed fish were more active than fed fish and made more swim bouts. Unfed fish were present in open waters (areas 2, 3, 5) and absent in area 6 regardless of prior experience.

Fed fish were much affected by early experience. Feeding acted to reinforce the influence of environmental imprinting. Deep-raised fed fish occurred in open waters more often than any other group. They also ranged vertically in areas 3, 5, 6 (day two) more than any other group and were in area 6 more often on day two. All deep-raised fish occurred in these areas but deep-raised fed fish occurred the most frequently because they were not being influenced by a higher drive of food getting and could then display more fully the affect of early experience. Shallow-raised fed fish were in areas 1, 4, 6 more often than any other group. Again this was due to prior experience and also because they were feeding off the substrate.

Since size and age cannot be naturally separated I choose to discuss them collectively. If I had tried to match 6-month old fish in size with 12-month old fish I would have skewed the natural curve. Therefore, age and size will both be considered in this part of the discussion. When 6-month fish were compared with 12-month fish it was found that 6-month fish were more closely associated with the substrate areas and mid-water areas (areas 4 + 5). Twelve-month fish were located in open waters and along the top surface of the water. Sale (1968) observed that as juvenile manini grow in size they move toward deeper water. This phenomenon has been observed by many scientists. It has been observed in the threadfin shad (Netsch, et al., 1971), the gizzard shad (Bodola, 1966), chinook and steelhead (Everest and Chapman, 1972), and glacier lantern fish (Halliday, 1967). Welcomme (1964) recorded a definite size depth correlation among Haplochromis species in Lake Victoria. The larger the fish the deeper the water column occupied. Usually, this change in depth of fish includes a movement away from the shore and into open waters. Stickney (1972) said that the magnitude of vertical migration in juvenile herring is smaller than the magnitude of adult vertical migration. Powles and Kohler (1970) suggest that this size spacing is a natural conservation mechanism for niche separation of adults and juveniles. The juveniles are better protected from predators in shallow water and are also able to obtain the right particle sized food. As the fish matures its abilities and needs change, and it moves into open waters to facilitate these changes. Hall, Cooper and Werner (1970) found that bluegills eat different particle sized food as they grow. There is also a change from planktonic feeding to benthos with growth. These changes are simultaneous with depth changes.

Day and Pearcy (1968) noted, in a study of species associations of benthic fish on the continental shelf and slope off Oregon, that depth range increases with the size of the fish. I suggest that my results indicate that older fish tend to occupy a broader range of depths. Because of this range in depth occupation, 12-month fish were not found to be in deep water area 6 any more often than were 6-month fish. In an experiment where fish had to choose between shallow and deep water with no opportunity of moving between depths I would predict that older fish would select deep water more often than younger fish.

In general, all 6-month fish behaved like shallow-raised fish, associating with the substrate; and all 12-month fish behaved like deep-raised fish, ranging in open waters both vertically and horizontally. These results are in concurance with restricted environment studies. If we consider that shallow-raised fish were reared in a restricted environment because they were not allowed to have experience with a very broad range of depths, then we could state that shallow-raised individuals were responding as restricted environment animals would respond. Harlow and Harlow (1962) showed that rhesus monkeys raised in a restricted environment confined their activities and associated only with areas with which they were familiar. Beach and Jaynes (1954) raised fish in dark aquaria and found that they did not show normal visual responses or orientation. The defects were not permanent.

If we consider that 6-month fish would naturally confine their activities to shallow water and remain in close association with the substrate as many young fish do; and if we consider that these activities would be restrictive to adult fish, then the correlation between 6-month and shallow-raised fish is explainable. Shallow-raised fish are responding as restricted (deprived) fish when they remain in close association with the substrate and do not venture into open waters. Deep-raised fish are responding as experienced or normal fish when they enter into open waters and range throughout the entire length and depth of the aquaria. This behavior would also be expected to be found in older fish as described earlier.

When the interaction between age and experience was considered the conclusions drawn above were strengthened. Deep-raised fish were little influenced by age. Deep-raised individuals were experienced individuals regardless of age and therefore would respond as fish that were raised in a normal environment where they had an opportunity to experience a range of water depths and distances from the substrate.

Age very much influenced the behavior of shallow-raised fish. As their age increased there was an increase in their presence in open waters and the top surface water areas. This means also that the fish were spending much less time closely associated with the substrate and more time ranging over the entire vertical length of the tank and exploring open waters. Here the effect of age is apparent. As with many animals, as a fish grows older it becomes "bolder" and begins to actively investigate areas that a younger fish would have avoided. This effect of age partially overriding prior experience could be very advantageous. The fish, by twelve months of age, are larger and more capable of maneuvering themselves in predator avoidance. Where small, young fish could protect themselves by swimming to shallow water cover, older larger fish would be too large to hide in much of the cover. Also, as pointed out earlier, the food type and particle size change with growth. The roach (Nikolsky, 1963) first consumes small, slow-moving plankton, then planktonic crustaceans, next benthic insect larvae, and finally, the adult food, molluscs. Pike young eat planktonic crustaceans, but soon the amount of energy expended on capture exceeds their calorific value and the pike start to feed on fish. Keast (1970) on noting that many piscivorous fish pass through periods of planktonic feeding, then insect-eating, before they become large enough to eat fish, stated that this is a mechanism whereby larger and smaller fish of the same species avoid food competion. Because these foods are present in different areas of water the young also avoid being eaten by the adults.

Experiment II

The results from the lighting effects experiment were rather surprising. Fish that were tested under shallow-dark

(SD) conditions avoided the shallow dark region (areas 1, 2, 4). They also avoided the entire shallow water region (areas 1-3) and the light-dark boundary. The fish tested under deep-dark (DD) conditions ranged over all areas of the aquarium avoiding only the light-dark boundary. Both SD and DD tested fish occupied area 6 more often than all-light (AL) tested fish. Although there was little difference between the responses of DD and AL tested fish, AL fish were in areas 1-3 and area 3 separately, more often.

Butler and Hawthorne (1968) noted that trout can be caught near objects of cover such as a boulder, an overhanging bank, a floating log or an area of turbulence. They stated that although the term, cover, is difficult to define, it does include the features of shade and shadow. Their experiments showed that rainbow trout, which were the most active trout tested, used cover the least amount of time; whereas brown trout, the least active, used cover the most often. Unfortunately, I did not measure the activity levels of the SD and DD fish.

If the fish were responding to the shaded areas of their aquaria as if they were cover, certain reactions could be expected. Sale (1969a.) determined that the depth selection of juvenile manini depended on the presence af adequate cover. Later, Sale (1969b.) found that although juvenile manini responded to light direction, the response was easily masked by other factors. Fish tested in deep water without cover spent more time in the upper half of the tank than did fish with cover. Fish tested in shallow water (their natural water depth) with cover made few exploratory and many feeding movements, while fish without cover made many more swim bouts and few feeding movements. If the <u>Haplochromis burtoni</u> were responding to the shaded half of their aquaria similarily, one would expect them to respond like shallow-cover tested manini under SD testing and like deep-cover tested manini under DD testing. This was not the case. The SD tested fish did not remain near the shallow-dark region exploring or anything else; they avoided that region. The DD tested fish did not spend more time in the upper half of the aquarium.

Kwain and McCrimmon (1966 and 1967) performed a series of tests to determine a fish's response to cover. Yearling rainbow trout showed a positive response to overhead cover at all light intensities tested. At .01 lux they swam little and remained under the cover; at maximum light intensity (200 lux) they swam actively but still remained under the cover most of the time. When the fish were tested for activity over black-bottomed tanks they swam randomly; over white-bottomed tanks they remained close to the periphery. When tested in a choice situation between black- and white-bottomed areas, they preferred black-bottomed areas only at .01 lux; the higher light intensities revealed a random distribution of trout between white- and black-bottomed areas. Ritter and MacCrimmon (1973a. and 1973b.) found that after 24 hours acclimation, only pond-reared fish still preferred black-bottomed areas (at 50 lux), while laboratory reared fish showed random distribution. They believe the response to black bottom color or overhead cover is a protective response and that active, unfearful fish are less likely to remain close to these objects. It might be assumed therefore, that lab-reared *Haplochromis burtoni*, after being acclimated for 24 hours, might respond as lab-reared rainbow trout and display random movement. This did not happen; the fish definitely avoided the darkened areas under SD testing and under DD testing the fishes' presence in the shallow-water region of the tank was less than AL tested fish.

Jones (1956) noted that minnows would not cross a light-dark boundary. This finding was similar to mine. The SD and DD tested fish avoided the light-dark boundary. Possibly one reason the SD fish were not present in the shallow-dark region was because they were reluctant to cross the light-dark boundary. To go into a shallow-darkened region which is the opposite of conditions usually found in nature where the deep regions are the dark ones, would be an unnatural response, so the fish would avoid the situation. In this experiment the fish avoided the shallow-dark region to such an extent as to avoid the entire shallow region. The DD condition would represent the more natural setup with the deep areas being darker, in fact darker than that depth of water usually is. However, this situation still represents a natural situation and therefore it would not be something to be avoided. The DD fish did not avoid the shallow-lit region of their aquarium either because it also represented a natural situation where the shallow water is lighter.

The use of artificial structures in attracting fish was studied by Klima and Wickham (1971). They found that the structure's position in the water column was important. Generally, more fish were associated with midwater structures than structures that were at the surface. Haines and Butler (1969) discovered that fish need a visual reference point in order to be attracted to cover. Virtually no use was made of any clear cover they employed although the covers were like the black covers in every other way and the fish were definitely aware of their presence. The situation under which the fish were tested in Experiment II may not have offered any visual reference point to the fish in the shaded areas and the "cover" was not only above the fish; it was completely out of the water. Therefore, the fish were not attracted to the darkened areas as if they represented cover. Perhaps the fish did not perceive the shaded areas as cover at all. In the SD condition perhaps the fish had been adapted to avoid shadows that could be potential predators. In the DD conditons a fish would not be as readily trapped if attacked from above; so perhaps this situation was not as potentially dangerous to the fish and was not avoided.

Another way to consider the results of Experiment II is in terms of the amount of attraction or avoidance to light. Stickney (1969) noted several factors influencing the attraction of herring to artificial light; among these were: temperature, position of the light, previous light adaption of the herring, as well as their age and physiological state. He found that attraction to light was greater at low temperatures. This seems adaptive if one considers that the fish were also seeking an optimum temperature range, which of course is influenced by sunlight. The attraction of artificial light was greatest if the lights were submerged. Bright light (20-600 lux) at, and especially above, the water surface tended to repel fish. Stickney also found much individual difference among the fish.

Many freshwater and marine animals have optimum light ranges. Pelagic species keep within this range by vertical and horizontal migration. Although the species are usually found within this light range, higher pressures can cause them to leave the ranges.

If the <u>Haplochromis</u> <u>burtoni</u> were being attracted to the artificial lights above their aquaria, the AL fish would be found in areas 1-3, as they were. However, the DD fish should have been present most often in the shallow-lit region, when in fact their distribution was random. Also SD fish, if they were being attracted to the artifical light above their aquaria, should have been in areas 2.5 and 3, which

were in fact avoided. Therefore, it appears that light attraction or avoidance was probably overruled by a higher pressure. This higher pressure appears to have been rather powerful in view of the fact that although the SD and DD tested fish were not fed, they either avoided the shallow-water region or were present there only randomly. As shown in Experiment I, hunger usually causes fish to seek food along the top surface of the aquaria just as AL tested fish did. The effect of shade somehow caused the fish tested with it to cease food seeking and distribute themselves differently.

Possible insight into their behavior can be gained through work done by Welcomme (1964). He found that *Haplochromis* have quite a low tolerance to high temperatures and therefore avoided the beaches of lakes during periods of high temperatures during the day. When the sky was overcast, or at night, the *Haplochromis* would return to the shallow beaches. If a fish was in the deep-lit part of the SD testing tank it would be responding as a *Haplochromis* during the day if it did not seek to venture into the shallow water. Under natural conditions all parts of a lake would be equally lit; so there would be no mechanism to attract the fish into shallow water. There would be no expectation that the shallow water would be darker and therefore cooler. This phenomenon, coupled with the fishes' avoidance of the light-dark boundary, would probably be sufficient to cause it to avoid not only the shallow-dark areas but also the

entire shallow water region. Conversely, a fish tested under DD conditions would be similar to a wild Haplochromis in a lake at night, or under overcast skys, or even natural conditions where deeper water is darker. There would be no reason for a fish in the deep-dark areas, especially areas 2.5, 3, 4.5 and 5 to anticipate that the beaches would be lit. Therefore the fish might even initially be attracted to the shallow-lit region. Once it entered the region, however, there would be a mechanism, high temperature avoidance, that would cause it to leave eventually. The end result of this behavior would be a type of approach-avoidance behavior that would appear as random behavior when it was analysed.

Application of the Research

Haplochromis are being used increasingly in the fisheries of Africa. The species are often difficult to separate and little is known of the genus let alone each species. Work (Fryer and Iles, 1972) is being done to trace the evolution of the cichlids of Africa but this is very difficult.

An understanding of why a species of fish behaves as it does makes it possible to predict what it will do in the future. By knowing the effect of early experience, feeding situation, age, temperature and light on the behavior of a fish species we can know how to influence these characteristics

for the benefit of people. Hatcheries have largely neglected to apply behavioral information. The fish are raised in barren, vary unnatural environments with no exposure to factors that may well dictate whether they will live or die soon after introduction into a natural habitat. Shuck (1948) and others (Miller, 1953 and 1958; Wales, 1954) noted that hatchery-raised trout do not survive well in streams. Shuck stated that because they have not had experience with a wide range of temperatures, live food and the opportunity to forage, predator avoidance, competition with other trout, and because they were too "tame", their survival was very short. Too high temperature acclimation (Eiffer, 1963) may also account for high mortalities of hatchery-raised trout. Because hatchery-raised Atlantic salmon spent much time in social interaction and less time feeding, they used up too much energy and increased their exposure to predators (Fenderson, Everhard, and Muth, 1968 and Fenderson and Carpenter, 1971). Vincent (1960) and Moyle (1965) both noted that domestic trout were less frightened of unfamiliar objects and did not seek cover. Also, domestic trout surfaced and moved through all levels of water, while wild fry tended to remain close to the bottom. Vincent hypothesized that this was because generations of domestic trout were raised in shallow water raceways and had been selected for low pressure. This factor alone could account for much of the increased mortality.

Some experiments have been conducted to improve the survivorship of hatchery-reared trout and salmon. Thompson (1966) studied the biological feasibility of training salmon to avoid predators and the effects of training on post-release survival. The avoidance response developed by these salmon served to reduce by one-half the rate of mortality of the trained fish when exposed to a standard predator population. Shetter and Cooper (1957) trained trout to (1) feed off the bottom, (2) feed off the bottom and avoid predators, (3) feed off the bottom, avoid predators and use cover. The conditioning made legal-sized trout less susceptible to capture by anglers during the first few days. The first few days are very important to the ultimate survival of the fish, and if a fish manages to live through those vital days, its potential for long range survival increases greatly. One of the potential predators the fish learned to avoid was a shadow. This type of avoidance directly related to Experiment II. If we wish to teach fish to avoid shadows, the depth of water where the shadow occurs is important as shown by the avoidance reaction of the fish to a shadow in shallow water and the lack of avoidance in deep water.

Also, experience with a range of water depths is important to young fish. If hatchery-raised fish respond as shallow-raised fish in Experiment I, they may not respond correctly when threatened by a predator or in food-seeking situations. The importance of food-seeking was also demonstrated in Experiment I. Because the fishes' food was introduced at the surface of the water, as it is in hatchery feeding, the hungry individuals were usually at the surface of the water. This behavior may also be dangerous in predator infested waters. It would probably be better to introduce live, natural food from the bottom or side of the raceway. I also found that age is important in depth preference; this is another factor that should be more closely examined with regard to hatchery-rearing fish.

Simons (1969) found that wild Atlantic salmon disperse over a greater area than hatchery-reared salmon. This lack of dispersal could also be involved with early experience in breadth and depth ranging. Perhaps hatchery-raised fish need greater depth range experience before they will disperse more.

Buss et al. (1970) described extremely high survival and production levels of fish raised in vertical units. In the vertical 1.66 gallon hatching jar maximum production was 7.7 pounds of fish in 6.2 pounds of water. In 16.5 feet high silos the production per cubic foot of rearing space was 8.53 pounds, far in excess of the normally accepted 1.5 pounds per cubic foot. The silos gave the fish much greater depth experience which may be a factor that would help insure greater survival. Behavioral research should be done to determine if this is true.

Suggestions for Future Study

As with most research, the experiments opened up the possibility for much more work that needs to be done. One of the first changes I would make with the experiments would be to increase the range of water depths. Since there were definite results with the small range of depths used in my experiments, it would be very interesting to know what results a greater range of depths would produce. I would use thermistors or photocells to continuously monitor a fish's movements throughout a 24-hour period. I would also be very interested in learning the effect of competition on depth behavior. In keeping with King's (1958) parameters I would like to find out when habitat imprinting is most strong and for how long a period of exposure would experience be necessary to gain lasting results in adult behavior.

Field work is definitely called for. The study of commercially important fish would be most directly beneficial. In the field I would like to learn the influence of predators, seasons (light and temperature changes), and natural sloping topographical features.

More behavioral data concerning the use of food and space would be most useful. I would like to work with the effects of natural vs. prepared foods on hatchery-reared fish. I believe that experience with natural food, properly introduced, could be very influential to the survival of hatchery-raised fish.

Finally, and perhaps most importantly, work needs to be done with hatchery management personnel. Furnishing the proper information and education for these people is absolutely necessary if the work done on habitat selection will ever be used commercially. I cannot overstate my conviction that a major difficulty faced by animal behaviorists is the lack of understanding between themselves and the people involved in practical application.

SUMMARY

1. Ninety *Haplochromis burtoni* were raised in either deep or shallow water until they were six or twelve months old. Thirty fish were raised until they were six months old; half of these were deep-raised, the other half were shallow raised. The fish were tested in experimental aquaria that consisted of a series of steps ranging in depth from the depth of the shallow conditioning tanks to the depth of the deep conditioning tanks. The fish were acclimated for 24-hours, then observed for three days. Their position was recorded every 15 seconds for ten minutes a day. Observations were also made of swim bouts and feeding movements. The six-month fish were not fed during the experiment. Fifteen of the deep-raised 12-month fish and fifteen of the shallow-raised 12-month fish were not fed during the experiment. The other thirty (fifteen deep-raised and fifteen shallow-raised) 12-month fish were fed daily during the three-day testing period.

2. Shallow-raised 12-month fish were found to appear significantly more often than deep-raised 12-month fish on substrate associated areas (1, 4, 6), and in area 1. It was suggested that because these fish had only experienced water

levels that kept them close to the substrate, the shallow-raised fish were remaining close to areas that were most familiar to them.

3. Twelve-month, shallow-raised fish made few swim bouts and many feeding movements.

4. Deep-raised, 12-month fish were in open waters (areas 2, 3, 5) and areas 3, 5, 6 (the longest vertical column) significantly more often than shallow-raised fish on all days. They were in areas 1-3 (the shallow water region) more often on day one and in area 6 (the deepest area) more often on day two. They occurred significantly more often in area 3 on day three. It may be that deep-raised fish, having experienced this range of water breadth and depth, were utilizing areas of the aquaria with which they were most familiar.

5. Deep-raised fish made more swim bouts and fewer feeding movements than shallow-raised fish. This was probably because they occupied areas convenient for swim bouts and where food particles would not settle.

6. When fed fish were compared with non fed fish it was found that fed fish were in areas 1, 4, 6 most often. Fed fish made many more feeding movements and fewer swim bouts than non fed fish.

7. Unfed fish were in areas 2, 3, 5 more often than fed fish for all three days. They were also in areas 1-3 more often on day one and day three. Unfed fish were more

active (made more swim bouts) and made fewer feeding movements than fed fish. This behavior was accounted for by the fact that not fed fish were moving through open waters, probably searching for food. Also, it would be a waste of energy for fish to make feeding movements when there was no food present; so the unfed fish did not make many feeding movements.

8. The interaction between experience and feeding situation was analysed. Unfed fish were little influenced by prior experience. Unfed fish avoided area 6 (probably because they were food-seeking elsewhere). Fed fish were influenced by early experience. Deep-raised, fed fish were in open water areas 2, 3, 5 most often of all groups on days one and two, shallow-raised fed fish were there least often of all groups. Deep-raised, fed fish were also in areas 3, 5, 6 most often of all groups on day two, shallow-raised, fed fish were there least often of all groups. Shallow-raised, fed fish occurred most often of all groups in areas 1, 4, 6 (on all days tested) and area 1 on day two. Deep-raised fed fish occurred in these areas least often. It therefore appears that feeding reinforces habitat imprinting while hunger overrides it.

9. Six-month fish were compared with 12-month fish. It was found that 6-month fish were associated with areas directly adjacent to the substrate (areas 1, 4, 6), while 12-month fish occurred more often in open waters (areas 2, 3, 5) and at the top surface (areas 1-3).

10. Regardless of age, all shallow-raised fish were substrate associated, while all deep-raised fish appeared significantly more often in open waters and areas 3, 5, 6.

11. When the interaction of age and experience was considered, it appeared that shallow-raised fish behaved like 6-month fish and deep-raised fish behaved like 12-month fish. However, when the interaction of age and prior experience was analysed, there was no influence of age on deep-raised fish. Age very much influenced the behavior of shallow-raised fish. Shallow-raised, 6-month fish were the most closely associated with the substrate; shallow-raised 12-month fish were found more often in open waters and along the top surface. Possible explanations for these differences were discussed.

12. All the fish used in Experiment II were deep-raised 12-month not fed fish. The AL (all lit) test was the same as the deep-raised 12-month not fed fish. The same experimental aquaria as used in Experiment I were used. For the DD (deep-dark testing, the deep half of the aquaria were darkened. The SD (shallow-dark) experiment had the shallow half of the aquaria darkened.

13. A chi-square analysis of areas in SD testing showed that the fish avoided the shallow darkened region, the light-dark boundary and areas 1-3. They occupied the deep areas of the aquaria.

14. Chi-square analyses of areas occupied by DD tested fish showed no difference in selection of either half of the aquaria. They occurred in areas 1, 2, 4 as frequently as other areas. The DD tested fish also avoided the light-dark boundary.

15. When SD tested fish were compared to AL tested fish it was found that AL fish occurred in areas 1, 2, 4 much more frequently than SD fish. SD fish occupied area 6 much more often than AL fish.

16. In a comparison of DD fish with AL fish, AL fish were shown to occur in areas 1-3 more frequently, while DD fish occurred in area 6 more often.

17. When DD fish were compared with SD fish no difference was found in the amount of time spent in area 6. DD fish appeared more often in areas 1, 2, 4 and areas 1-3 than SD fish.

18. Possible explanations for the behavior of the fish were discussed.

19. The applied aspects of the research were discussed and future study was proposed.

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