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ISBN 0-315-60595-2



UNIVERSITÉ D'OTTAWA
UNIVERSITY OF OTTAWA

**This thesis is dedicated to my mother Late Zaibun Nisan Begum and
my father Mr. Irtaza Husain Ansari whose blessings and prayers
gave me the strength and courage to
complete this thesis.**

ACKNOWLEDGEMENT

First of all I wish to thank my thesis supervisor Dr. S. U. Qadri, for his guidance and help during this project. This work was not possible without his consistent guidance and encouragement.

A member of my research committee, Dr. Don E. McAllister, provided the necessary restraint for my enthusiasm. His help in obtaining assistance for the field work is especially appreciated.

The other members of my research committee Dr. J. Picman and Dr. B. Fenton helped me much in working out the experimental designs and the statistical procedures for this study. Dr. D. Smith provided instrumental comments in organising to write this manuscript.

The computer programming for data analysis was helped by Dr. P. Lefkovitch and Dr. D. Debrowski. I am thankful to them for their time and interest in this project.

I wish to thank my fellow graduate students: C. B. Renaude, T. Edge and L. Lejoa who were always willing to help me in the field and laboratory.

My brother Dr. Iqbal Husain was a source of care, affection and encouragement to me and I would always be thankful to him for his support. My other brother Prof. J. H. Ansari and sisters Dr. Naushaba Murad and Dr. Ruqaiya Hussain supported me morally to finish this work.

Finally, I would like to thank my wife Lalin for all the encouragement, patience and help she had to give, while, I was doing this work. She also helped me in typing up this manuscript. My son Waseem Ansari has been a source of pleasure and happiness to me.

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ABSTRACT

Variation in feeding behaviour was studied among young individuals of pumpkinseed (Lepomis gibbosus) and yellow perch (Perca flavescens). Three types of food, Drosophila, Daphnia and Artemia were used for the experiments. Eight individuals of pumpkinseed differed significantly in their number of feeding attempts, in time interval between feeding attempts (in the beginning, middle and towards the end of the experiment), feeding angle, number of unsuccessful attempts and regurgitations. Most of the differences in the time interval between feeding attempts were observed in the middle and towards the end of the experiment. When the experimental diet was composed of three types of foods (Drosophila, Daphnia and Artemia) in a mixture, the total number of feeding attempts in the experiment decreased. Mixing the food types also reduced the feeding efficiency of individuals which was evidenced by the increased time interval between the feeding attempts and the increased unsuccessful attempts and regurgitations. Individuals of pumpkinseed showed the highest preference for Daphnia. On the basis of the above feeding variables, groups of individuals of differing feeding patterns were identified.

Similar patterns were observed for the eight individuals of yellow perch. Perch fed more efficiently on Artemia, however, two individuals of perch were more efficient on feeding on Daphnia.

Effects of the presence of conspecifics and increasing population density were examined on the variation among individuals of the pumpkinseed and yellow perch, for two types of food, (Daphnia and Artemia), separately and in a mixture. The effects of conspecifics were not equal on each individual of pumpkinseed and yellow perch. Only the weaker individuals were affected more by the presence of other conspecifics than the stronger ones. The increasing population density of conspecifics increased the variation among the individuals of both species.

The effect of the presence of heterospecifics (yellow perch) were also examined on individuals of pumpkinseed for similar food types and feeding variables. At low experimental densities the effects of the heterospecifics were not significant. However, at high densities yellow perch affected the feeding behaviour of pumpkinseed individuals significantly. The effects of conspecifics on pumpkinseed were always greater than heterospecifics. Yellow perch did not affect the feeding behaviour of all the individuals of pumpkinseed equally.

Résumé

La variation dans le comportement d'alimentation fut étudiée parmi de jeunes individus de crapet-soleil (Lepomis gibbosus) et de perchaude (Perca flavescens). Trois types d'aliments (Drosophila, Daphnia et Artemia) furent utilisés dans les expériences. Une différence significative fut observée chez huit individus de crapet-soleil quant à leur habilité à faire des essais de capture, l'intervalle de temps entre ces essais de capture (au début, au milieu et à la fin des expériences), l'angle d'attaque et le nombre d'essais de capture échoués et de régurgitations. La majorité des différences dans l'intervalle de temps entre les essais de capture furent observées au milieu et à la fin des expériences. Lorsque la diète expérimentale était composée des trois types d'aliments (mélange de Drosophila, Daphnia et Artemia) le nombre total d'essais de capture diminuait. Le mélange des types d'aliments réduisait également l'efficacité d'alimentation des individus et ceci est démontré par l'accroissement dans l'intervalle de temps entre les essais de capture et l'accroissement dans le nombre d'essais de capture échoués et de régurgitations. Les individus de crapet-soleil démontrèrent la plus grande préférence pour Daphnia. En se basant sur les paramètres d'alimentation ci-haut des groupes d'individus ayant des schèmes d'alimentation différents furent identifiés.

Des résultats similaires furent observés chez les individus de perchaude. La majorité des individus de perchaude démontrèrent

une préférence pour Artemia. Toutefois, deux individus de perchaude se nourrissaient de Daphnia de façon plus efficace.

Les effets de la présence de conspécifiques et l'accroissement de la densité de population furent examinés quant à la variation entre les individus de crapet-soleil et de perchaude pour deux types d'aliments, Daphnia et Artemia, individuellement et mélangés. Il fut observé que les effets des conspécifiques n'étaient pas identiques chez tous les individus de crapet-soleil et de perchaude. Les individus les plus faibles étaient plus affectés par la présence de conspécifiques que l'étaient les plus forts. L'accroissement de la densité dans la population de conspécifiques augmentait la variation chez les individus des deux espèces.

Les effets de la présence d'hétérospécifiques (perchaude) furent également examinés chez les individus de crapet-soleil pour les mêmes types d'aliments et les mêmes paramètres d'alimentation. A de basses densités expérimentales, les effets des hétérospécifiques n'étaient pas significatifs. Toutefois, à de fortes densités expérimentales les perchaudes affectaient le comportement d'alimentation des individus de crapet-soleil de façon significative. Les effets des conspécifiques étaient toujours plus grands que les effets d'hétérospécifiques. La perchaude n'a pas affecté le comportement d'alimentation de tous les individus de crapet-soleil de manière identique.

CHAPTER I
INTRODUCTION

Individual differences in behaviour have largely been ignored, treated as white noise, or considered to be maladaptive deviations from optimal strategies (Magurran 1986; Arak 1984; Ringler 1983; Rubenstein 1981). In part this ignorance has come from the attempts of ecologists to explain interactions by relying on simple mathematical models (Rubenstein 1981). Models such as derivations of the logistic model of single species dynamics assume: (i) that all individuals in a population compete as equals and (ii) that the competitive ability of an average individual is unaffected by the density of the population. It is often realized by ecologists that the above conditions are rarely met but they ignore the discrepancy and presume that the models to be robust and that differences cancel each other out.

Studies on the feeding behaviour, growth patterns and reproductive performance of fishes have shown that significant variation among individuals of single species population exists and often leads to important ecological consequences (Bryan and Larkin 1972; Ringler 1975; Randolph and Clemens 1976; Rubenstein 1981; Ringler 1983; Ringler and Brodowski 1983; Magurran 1986).

The individuals of brook charr (Salvelinus fontinalis), cutthroat trout (Salmo clarki) and rainbow trout (Salmo gairdneri) differed significantly in their short and long term food specialization (Bryan and Larkin 1972). This specialization was not related to the size, growth rate, weight of food eaten or the site of recapture. Similar patterns were observed in the laboratory and

different searching behaviour, capturing techniques and feeding rhythms seemed to cause such intraspecific variations.

Rubenstein (1981) showed that significant variation in the growth rate and reproductive potential existed among the individuals of Everglades pygmy sunfish (Elossoma evergladei) and this variation was magnified when the population density of pygmy sunfish increased. Rowland (1982) observed that the individual males of three spine stickleback (Gasterosteus aculeatus) differed significantly in their response to colour by attacking red dummies at different rates.

The tolerance limits for temperature and the oxygen concentration were observed to differ among individuals of channel catfish (Ictalurus punctatus) by Randolph and Clemens (1976). The ranges of these limits were so broad that average values of both parameters were not applicable to many individuals of the same population.

Chesson (1978) and Lominicki (1978) developed structural models to show how within and between individual variation could contribute to patch variability and unequal resource partitioning among the conspecifics, thereby directly affecting the local population dynamics. Lominicki (1978) suggested that unequal resource partitioning among the individuals of a single species increases the stability of a confined population and allows the emigration of some members into suboptimal and hostile areas to

evolve by individual selection. The individual variation among conspecifics has often been observed as an established dominance hierarchy between distinct alpha, beta and gamma type individuals (Yamagishi et al. 1974; Li and Brocksen 1977).

The above studies show that individuals in a population may differ significantly from each other and factors such as increasing population density and the presence of other conspecifics or heterospecifics may affect the degree of within and between individual differences. It is increasingly believed now that focusing on individuals may provide a greater insight in the structure of biological communities (Root 1967). Variation in individual's abilities, irrespective of species, may be more important in determining the interspecific relationships than are average taxonomic differences (Wilbur 1976). In spite of the above studies, the role of individual variation during various intra- and interspecific interactions is not understood.

Fish populations are often food limited and their growth rates, in part, depend upon the food utilization patterns of individuals. Unfortunately, very few studies have been done to gather information on the individual variation in the feeding behaviour of fishes (Ringler 1983). This study was performed to examine variation in the feeding behaviour among the young individuals of pumpkinseed (Lepomis gibbosus) and yellow perch (Perca flavescens). Individual variation during intra- and interspecific feeding interactions of pumpkinseed and yellow perch

was also examined. These two species co-occur in many water bodies in the Great Lakes area and appear to affect the diet selection patterns of each other (Clady et al. 1972; Keast 1977; Hanson and Leggett 1985; Nakashima and Leggett 1985). Pumpkinseed and yellow perch were also abundant in the Kettle Island Bay area of Ottawa River near the city of Ottawa, Ontario where the specimens for this study were obtained. The following questions were investigated during this study:

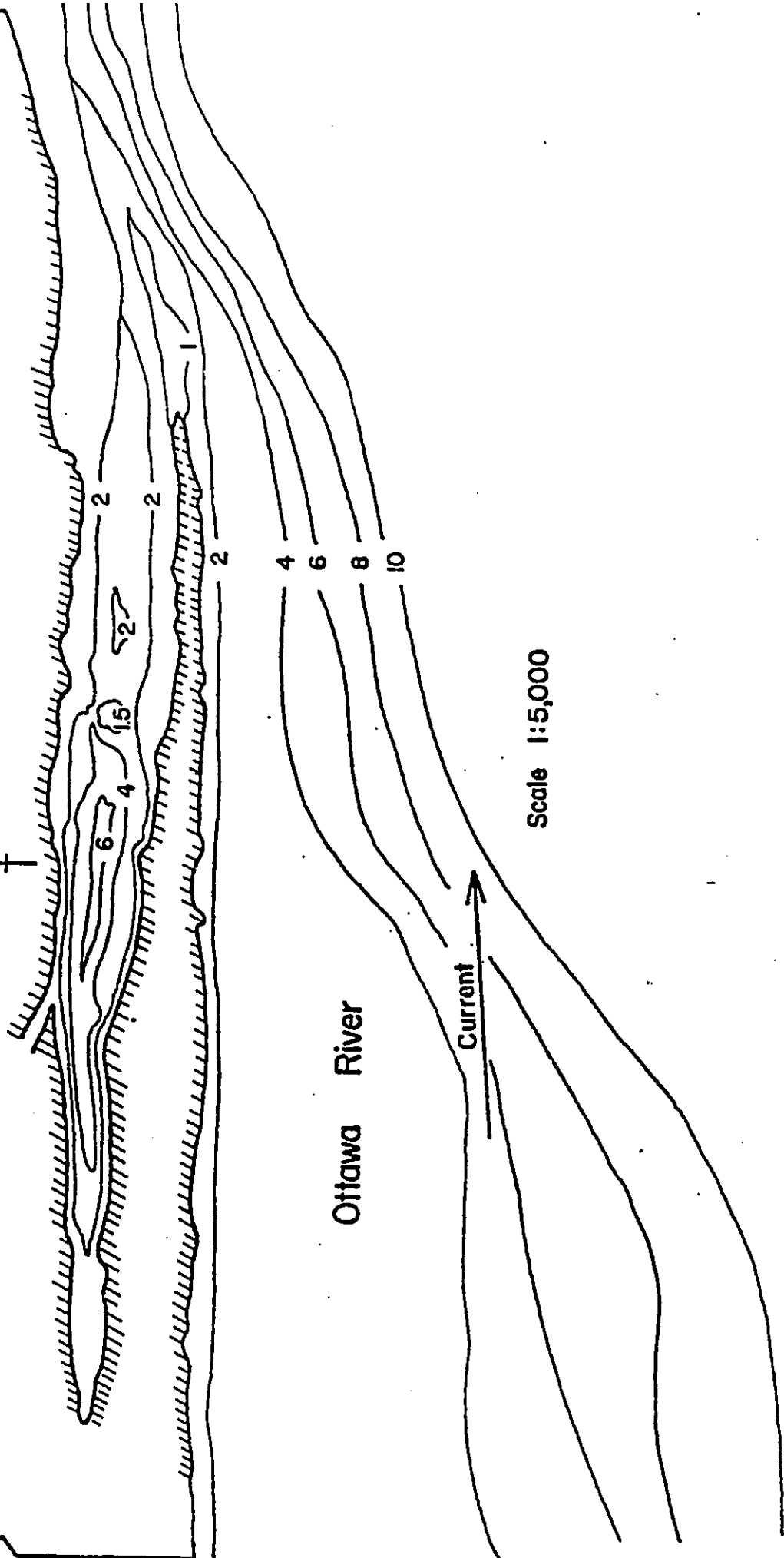
- i) Does significant individual variation exist in the feeding behaviour of pumpkinseed and yellow perch?
- ii) Does increasing population density affect the degree of individual variation?
- iii) Are all the individuals of pumpkinseed and yellow perch affected equally during the intra- and interspecific interactions?

Attention was focused on the foraging abilities of the above two species in terms of selected feeding variables (see materials and methods).

CHAPTER II
DESCRIPTION OF STUDY SITE

Figure 1. Depth contours of Kettle Island Bay in meters

KETTLE ISLAND



Scale 1:5,000

Ottawa River

Current

Young specimens of pumpkinseed and yellow perch were obtained from Kettle Island Bay of Ottawa River, at Ottawa, Ontario (75° 39' 0" W 45° 28' 8" N). This is a narrow bay approximately 5 ha in area (Fig 1). The topography and vegetational structures are quite different at the two ends. The east end of the bay which joins with the Ottawa River is wider than the west end and has an average depth of 1.5 m with abundant vegetation. Marginal trees in this part are tall but not as dense as in the west end. The bottom in the east end is mainly sandy because of the sand particles brought by the river currents. The middle part of the bay is the deepest part (up to 6 m deep), but the bottom is mostly muddy and covered with leaves fallen from the marginal trees. The west end is very narrow and shallow (0.5 to 1 m deep) and is full of logs. The light is also low in this part because of the tall marginal trees. Water plants and vegetation are scattered throughout the bay and vary in densities. Dense vegetation is present only close to the shore line up to the depth of about 2 m in the middle and wide part of the bay but towards the shallow end the vegetation occupies the whole water area. In general Kettle Island Bay provides excellent habitat for fishes that enter the bay in early summer for spawning. The dense vegetation in several parts of the bay protect young fish from potential predators.

The fishes used in this study were mainly caught at the east end of the bay close to main Ottawa River from the dense vegetation area. Other species of fish observed in the bay close to and at the collection site were largemouth bass (Micropterus salmoides),

minnows (Hybognathus regius, Notemigonus crysoleucas, and Notropis atherinoides), rock bass (Ambloplites rupestris) and northern pike (Esox lucius).

Emergent vegetation at the collection site consisted of Sagittaria latifolia, Scirpus atrovirens, Polygonum natans, and Pontederia cordata. Dense growths of Elodea canadensis, with varying amounts of Ceratophyllum demersum and Vallisneria americana to a depth of about 1m were observed. Thick patches of Potamogeton natans, P. crispus, P. perfoliatus and P. pectinatus grew with some Vallisneria and Ceratophyllum from about 1 to 2.5 m depth. Nymphaea odorata and Nuphar variegatum grew with the potamogeton species on two underwater humps at 1.5 and 2.0 m depths as well as across the mouth of the bay. Scattered patches of Myriophyllum heterophyllum and Comba caroliniana were found throughout the bay.

The physical and chemical characteristics of water in the study area were studied by Hanson (1980 and are shown in Table 1.).

CHAPTER III
MATERIALS AND METHODS

Quantitative and comparative observations on the feeding behaviour of pumpkinseed and yellow perch were made in the laboratory. Behavioural responses of the individuals of these two species were examined for three different food types: dead adult Drosophila melanogaster floating on the surface, live Daphnia magna in the water column and frozen Artemia salina lying at the bottom. These foods were selected for the following reasons: i) they occupy three feeding habitats (surface, mid-water column and bottom) available to fishes in their natural environment, ii) they are readily accepted by both the species, iii) Daphnia and Drosophila are easily cultured in the laboratory and Artemia is obtained commercially. Individuals of pumpkinseed and yellow perch showed more preference for Daphnia and Artemia. Therefore, Drosophila was discarded from the later series of experiments.

3.1 Feeding variables

The feeding behaviour of fishes was measured by the following variables:

i) Number of feeding attempts:

Detection of a food item in the tank by the fish followed by an approach and an encounter. The result of an attack (success or failure) was not considered in this variable.

(ii) Time interval between feeding attempts:

This variable was used to measure the feeding intensity of the two species at the beginning, middle and

towards the end of the experiment (i.e. after 1, 3, and 7 minutes from the start of the experiments). At each phase, five to seven observations of feeding attacks were made and the time intervals between these attacks (in seconds) were used to analyse the data for this variable.

(iii) Unsuccessful attempts:

The fish attacked a food item and was not able to capture it. This usually happened when fish tried to attack two food items at the same time and missed both of them, angle of the attack was not correct, or the food item moved away with fish's own swimming activity (visual observations during the study).

(vi) Regurgitation:

In some cases the fish made a successful attempt and the food item was captured but (for some unknown reason) the fish spat out the food item(s) immediately or some time after the capture.

(v) Feeding angle:

Angle between the fish's longitudinal body axis and the horizontal plane in the water column in which the food item was present at the time of attack. Measurements on feeding angles were always taken in similar ways to maintain the consistency.

The above variables were selected to measure the foraging abilities of pumpkinseed and yellow perch. These variables have often been considered important in determining the feeding success of fishes (Ringler 1983, Cooper et al. 1985). A fish was

considered to be a better feeder if it made high number of attempts, low numbers of unsuccessful attempts and regurgitations and finally it sustained active feeding (low time interval between feeding attempts) during most of the experimental time period.

3.2 Collection of fish specimens

The young pumpkinseed and yellow perch (4.0- 7.0 cm in total length) were collected by a seine net (30.5 x 1.8 m with 64 mm mesh and 1.8 m pocket) in September of 1985. The two species were held separately in two large aquaria (90 x 180 x 90 cm) under 14:10 h light:dark photoperiod and maintained at 12° C for one month and fed shrimp pellets obtained from a local pet shop. These tanks had a chlorine-free running water supply.

3.3 Acclimatization to the laboratory conditions

Eight experimental individuals of pumpkinseed and yellow perch (7.0- 8.5 cm total length) were then removed from the holding tank and transferred to the laboratory aquarium at a gradually raised temperature from 12° to 19° C. Light conditions in the laboratory were similar to those of the holding tank, and fish individuals were fed the experimental food items (dead Drosophila, Daphnia and Artemia). These three food types were fed in a random order to avoid any conditioning for food. Mills (1987) showed that young yellow perch were not conditioned to a familiar prey type if provided with a prey item of better nutritional quality. All the

Table 1. Average values of physical and chemical variables of Kettle Island Bay, 0.1 m beneath the surface during 1978 and 1979.

Variable	Number of samples	Mean + S.E.	Range
pH	22	7.22 ± 0.04	6.9- 7.6
Total hardness	22	30.77 + 1.39 Ca CO ₃	20.0- 45.0
Carbon dioxide	22	7.95 ± 0.19 mg/l	4.0-12.0
Dissolved oxygen	22	8.44 ± 0.19 mg/l	7.0- 11.0
Conductivity	4	58.75 ± 2.93 uMhos/m	52.0-65.0

(Source: Hanson 1980)

experimental fish individuals were acclimatized to the above laboratory conditions for three weeks prior to the experiments.

3.4 Experimental procedures

Preliminary experiments

Preliminary experiments were performed to select the following experimental conditions:

i) Size of the aquarium. Information provided by Martin (1975) and Sprague (1973) was also used for this selection. ii) light conditions during the experiments. iii) marking method for the identification of fish individuals. iv) marking of experimental tank to assess the location of fish in the water column (surface, mid-water column and bottom). v) location of the video camera to obtain the best views of the experimental individuals. vi) location of the experimenter to minimize the disturbance to the experimental fish and vii) food density for each experiment. To do this one food type was offered to one fish ad-libitum and after 15 minutes its gut was opened to see the amount of food eaten by the fish. After examining the 15- minutes- feeding capacities of three similarly size fish, an average food amount was calculated. A similar procedure was followed for each food type. The above food density selection method was used to make sure that fish individuals received sufficient food during the experiments. viii) and finally to select the degree of aeration in the experimental tanks. The selected experimental conditions are

described below.

Protocol

Sudan Black (Fisher Scientific Co. C.I. No. 26150) stain was used for the identification of individual fish. 1 g of Sudan Black was dissolved into 1 ml of acetone and approximately 0.1 ml of this solution was injected into the fish skin just below the scales. This produced a little black spot on the fish body and was visible for up to two weeks. Mostly the caudle peduncle, the base of the dorsal fin, or the right or left abdomen were used for staining. Preliminary experiments showed that this method did not affect the feeding behaviour of fish. All the experimental fish were starved for 24 h before the experiments to standardize the level of hunger.

All the experiments were performed in 38 l aquarium containing chlorine- free tap water. Experimental tank was covered with white plastic sheets on three sides to prevent the visual interactions with other fishes in the nearby tanks. The experimental tank was partitioned into two compartments by a transparent plastic plate. At the beginning of the experiment the fish was introduced into the left half and food items were placed in the right half. After 5 minutes of acclimatization the partition was removed and the observations began.

The first series of experiments (described in chapter IV) were done on eight individuals of pumpkinseed. Same individuals were used for all the experiments of this series. Each individual was examined for its feeding behaviour (in terms of the above mentioned variables) for three food types separately and in a mixture. Three trials for each individual were performed for each food type. Therefore, each individual was tested twelve times for three food types and their mixture. However, more observations for each individual were taken for time intervals in the beginning, middle and towards the end of the experiments, as these intervals were measured between five to seven consecutive feeding attacks at each phase of the experiments. Equal quantities of Drosophila, Daphnia and Artemia were used in all the experiments. Average wet body weight of eight experimental individuals of pumpkinseed were calculated and 22.6 mg/g of fish body weight of each food type was used in the experiment. In experiments in which the mixture of three food items was used three food types were mixed in equal proportions, so the food density in these experiments were three times higher than other experiments which were performed on an individual food type. Experiments were performed in a random order to reduce the effects of learning for a particular food type.

Data were recorded with a programmable JVC colour video camera having a stop watch function and zoom lens (model no. GX-N70U), and a recorder (model no. BR-6200U). Experiments were performed under a cool white light (40 W) suspended 256 cm above the experimental tank. The camera was on a tripod in front of the uncovered side

of the aquarium and handled by remote control. Fish activity was also observed on a 36 cm colour monitor attached to the video recorder. The experimenter was always seated out of the sight of the experimental tank. The video recording of an experiment was replayed later and observations on the above variables were taken.

3.5 Statistical methods

Two kinds of statistics were used to analyze the data. Data for time interval between feeding attempts in the beginning middle and towards the end of the experiment were normally distributed and had a homogeneous variance, hence analysis of variance was used. A two-way analysis of variance was used. The time intervals were analyzed for eight fish individuals, three food types, and three replicates. For the unsuccessful feeding attempts, regurgitations, and feeding angles (where measured) the distributions were not normal, for these variables Logit analysis (parametric statistics) was used.

CHAPTER IV
INDIVIDUAL VARIATION IN THE
FEEDING BEHAVIOUR OF
PUMPKINSEED (LEPOMIS
GIBBOSUS) AND YELLOWPERCH
(PERCA FLAVESCENS)

4.1 Results

4.1.1 Pumpkinseed:

Mean values for time intervals between feeding attempts, for three types of food Drosophila, Daphnia and Artemia (Fig. 2) showed that eight individuals of pumpkinseed differed from each other. Most of the differences were observed in the middle and towards the end of the experiments (time ranges 5.94-17.44 and 11.39-28.73 seconds, respectively). Analysis of variance also showed similar results (Table 3). Higher F values were obtained for the time interval between feeding attempts in the middle (19.26, $P < 0.0001$) and towards the end of the experiments (36.67, $P < 0.0001$).

Differences in the feeding angles were more pronounced in the mid-water column (range 18.02-48.74°) than at the surface or at the bottom (Fig. 3).

Mean values for the number of feeding attempts for three types of food and their mixture also showed variation among eight individuals of pumpkinseed (Fig. 4). The number of feeding attempts ranged between 6.8-29.2 (Drosophila), 89.6-151.6 (Daphnia) and 70.0-114.3 for Artemia. For the mixture of these three food types a lower range for feeding attempts was observed (31.33-69.67) than food types used separately.

Individuals of pumpkinseed also differed for unsuccessful attempts and regurgitations (Figs. 5, 6 for mean values and Table 4 for logit analysis, respectively). Most of the individuals showed highest percentage of unsuccessful feeding attempts and regurgitation for Artemia.

The mean values for time interval between feeding attempts for eight individuals of pumpkinseed and three food types separately and in a mixture (Table 5), number of feeding attempts (Fig. 4) and percentage of unsuccessful attempts (Fig. 5) show that when fish individuals were offered a mixture of three food types the number of feeding attempts decreased and both, the time interval between feeding attempts and unsuccessful attempts increased. The diet composed of a mixture of three food types (Drosophila, Daphnia and Artemia) had a three times higher food density than when these food types were used separately. The results for Drosophila are excluded from discussion because it was eaten by fish only in small quantities.

4.1.2 Yellow perch:

Results similar to those for pumpkinseed were observed for eight individuals of yellow perch and two types of food, Daphnia and Artemia, separately and in a mixture.

Mean values for time interval between feeding attempts in the beginning, middle and towards the end of experiments show that individuals of differing foraging rhythms were present (Fig. 7).

Individual 1 and 3 fed actively in the beginning and middle of the experiment. But later on, towards the end of the experiment they became passive. Individuals 4 and 5 fed actively throughout the experimental time (10 minutes). Individuals 2 and 6 were passive at all phases. The rest of the individuals were intermediate in their foraging rhythms. Analysis of variance also showed significant variation among eight individuals of yellow perch for the time interval between feeding attempts for two types of food (Daphnia and Artemia) separately and in a mixture (Table 6).

Mean values for number of feeding attempts for eight individual yellow perch also showed some interesting results (Fig. 8). Most of the individuals made the highest number of feeding attempts on Artemia. Individuals 2 and 8 showed a greater preference for Daphnia than Artemia. Individuals 2 and 8 also made fewer unsuccessful attempts and regurgitations for Daphnia (Figs. 9 and 10). The number of feeding attempts decreased when individuals were exposed to a mixture of Daphnia and Artemia.

A logit analysis shows (Table 7) shows that individuals of yellow perch differed significantly for number of unsuccessful attempts and regurgitations. An examination of unsuccessful attempts and regurgitations (Figs. 9 and 10) shows that most of the individuals (except 2 and 8) made more unsuccessful feeding attempts for Daphnia than for Artemia. The unsuccessful attempts were generally high when fish were exposed to a mixture of Daphnia and Artemia. The majority of fish individuals made more regurgitations for Daphnia than Artemia (Fig 10).

Table 2. The experimental conditions selected for this study.

Food type	Quantity of food used (mg/g fish body mass)	Number of trials	Experimental duration (minutes)
<u>Drosophila melanogaster</u>	22.60	3	10
<u>Daphnia magna</u>	22.60	3	10
<u>Artemia salina</u>	22.60	3	10
Mixture of above three	3 X 22.60	3	10

Table 3. Time interval between feeding attempts in the beginning, middle, and towards the end of the experiments for eight individuals of pumpkinseeds and three types of food (Drosophila, Daphnia and Artemia) separately and in a mixture.

Time interval between feeding attempts	degrees of freedom	F	P<
In the beginning of experiment i.e. after 1 minute from the start of the experiment	7, 559	4.09	0.0002
In the middle of experiment i.e. after 3 minutes from the start of the experiments	7, 549	19.26	0.0001
Towards the end of the experiment i.e. after 7 minutes from the start of the experiment	7, 491	36.67	0.0001

Analysis of variance was used

Table 4. Number of unsuccessful attempts and regurgitations for eight individuals of pumpkinseed and three types of food Drosophila, Daphnia and Artemia, separately and in a mixture.

Feeding variables	Degrees of freedom	Chi-square	p<
Number of unsuccessful attempts	7	27.50	0.0001
Number of regurgitations	7	194.76	0.0001

Logit analysis was used

Table 5. Average time interval between feeding attempts for eight individuals of pumpkinseed and three types of food separately and in a mixture. Means are followed by standard errors.

Food type	Average time interval between feeding attempts (secs)
<u>Drosophila</u>	16.50 \pm 1.44
<u>Daphnia</u>	5.35 \pm 1.48
<u>Artemia</u>	3.53 \pm 1.48
Mixture of the above three	10.96 \pm 3.17

Table 6. Time interval between feeding attempts in the beginning, middle and towards the end of the experiment for eight individuals of yellow perch and two types of food Daphnia and Artemia separately and in a mixture.

Time interval between feeding attempts	Degrees of freedom	F	P<
In the beginning of experiment i.e. after 1 minute from the start of the experiment	7, 417	4.58	0.0001
In the middle of the experiment i.e. after 3 minutes from the start of the experiment	7, 417	13.48	0.0001
Towards the end of the experiment i.e. after 7 minutes from the start of the experiment	7, 373	16.65	0.0001

Analysis of variance was used

Table 7. Number of unsuccessful attempts and regurgitations for eight individuals of yellow perch and two types of food Daphnia and Artemia, separately and in a mixture.

Feeding variables	Degrees of freedom	Chi-square	P<
Number of unsuccessful attempts	7	28.68	0.0001
Number of regurgitations	7	37.83	0.0001

Logit analysis was used

Figure 2. Mean values for time interval between feeding attempts in the beginning, middle and towards the end of the experiment for eight individuals of pumpkinseed and three food types Drososphila, Daphnia and Artemia and their mixture.

Time interval (secs)

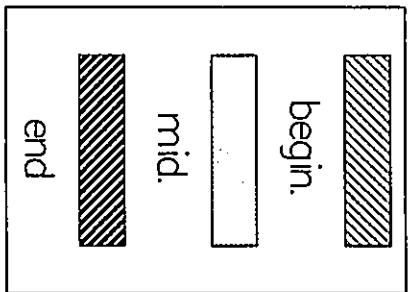
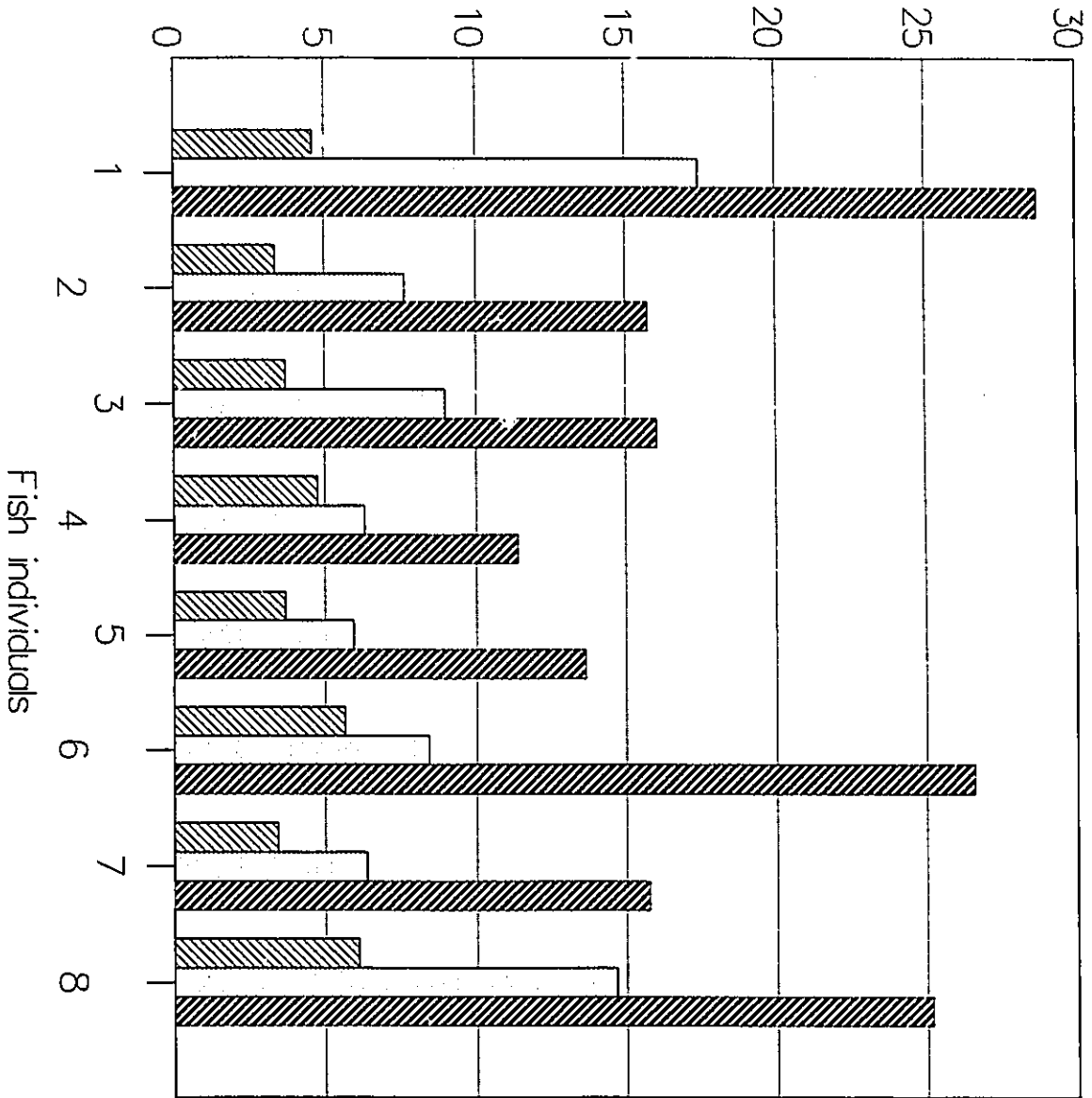


Figure 3. Mean values for feeding angles at the surface (for Drosophila), in the mid-water column (for Daphnia) and at the bottom (for Artemia) for eight individuals of pumpkinseed.

Feeding angles (degrees)

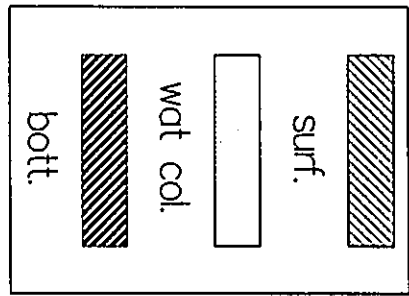
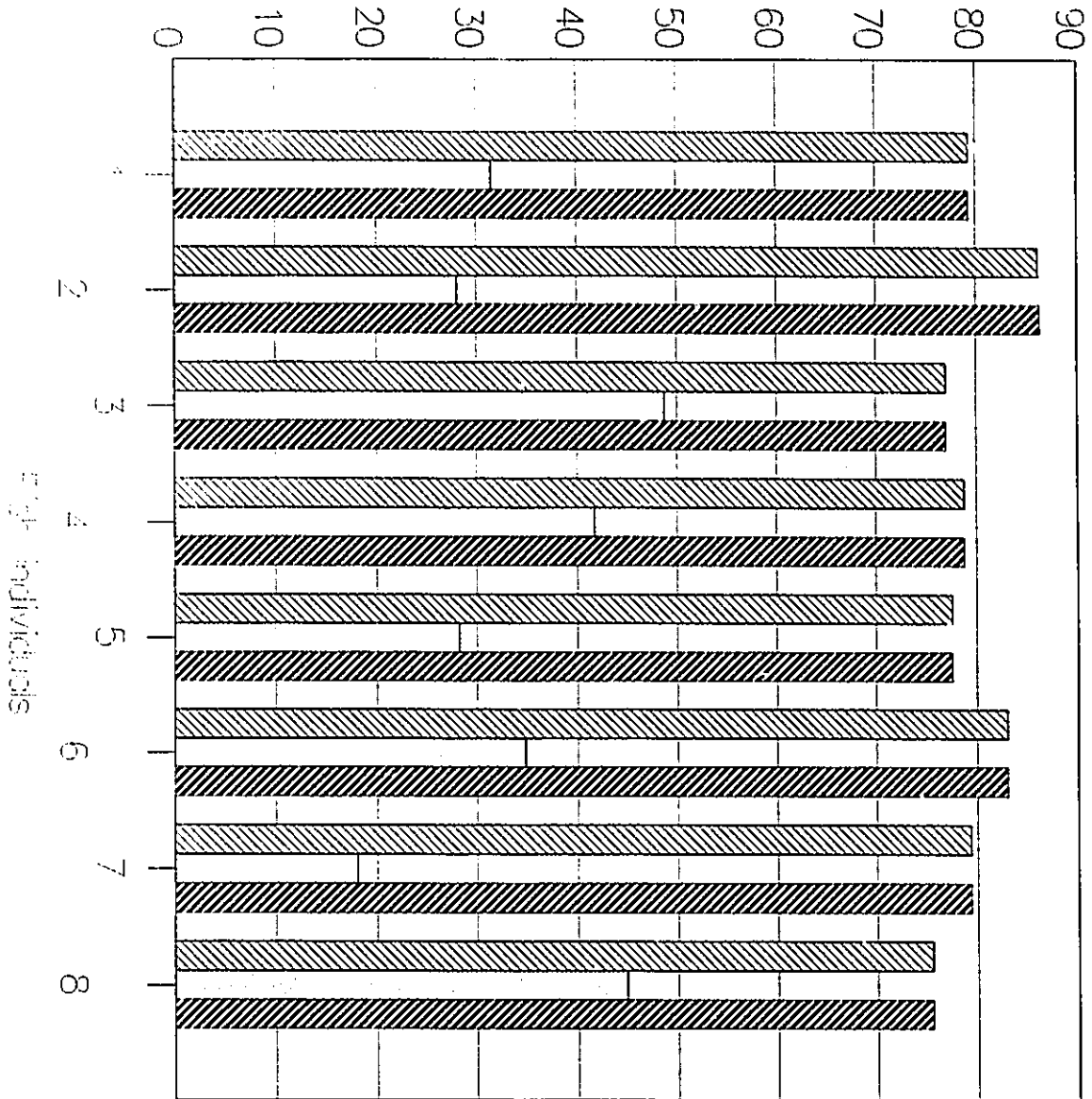


Figure 4. Mean values for total number of feeding attempts made by eight individuals of pumpkinseed for three food types Drosophila, Daphnia and Artemia and their mixture.

Feeding attempts (No.)

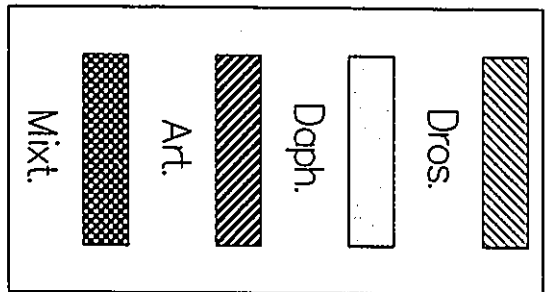
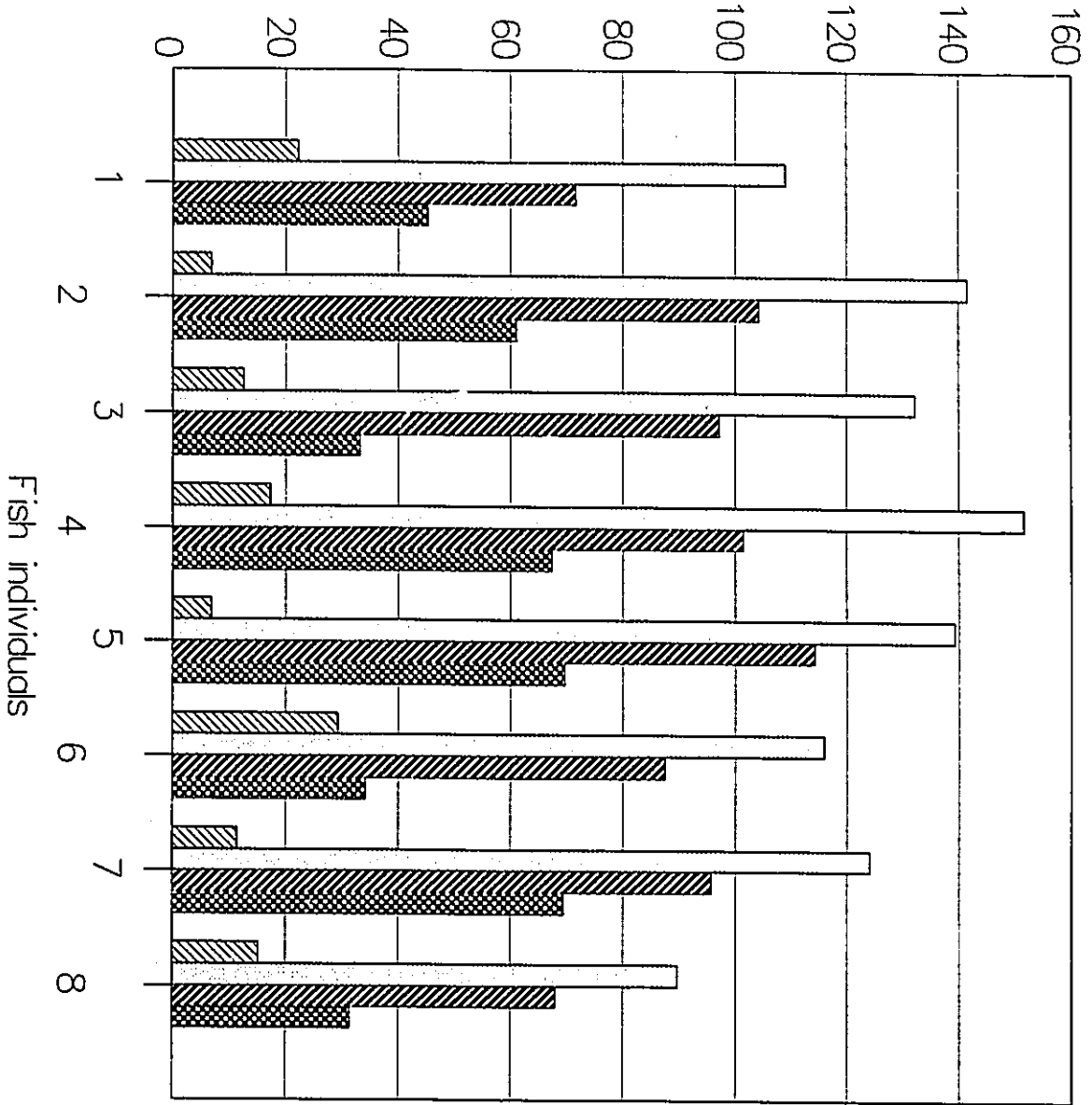


Figure 5. Mean values for the number of unsuccessful attempts (%) made by eight individuals of pumpkinseed for Daphnia and Artemia and their mixture.

Unsuccessful attempts (%)

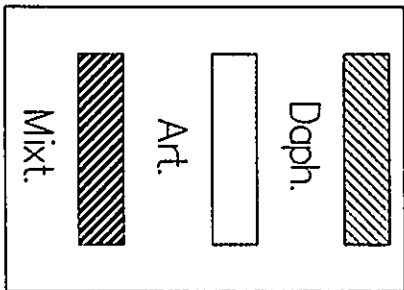
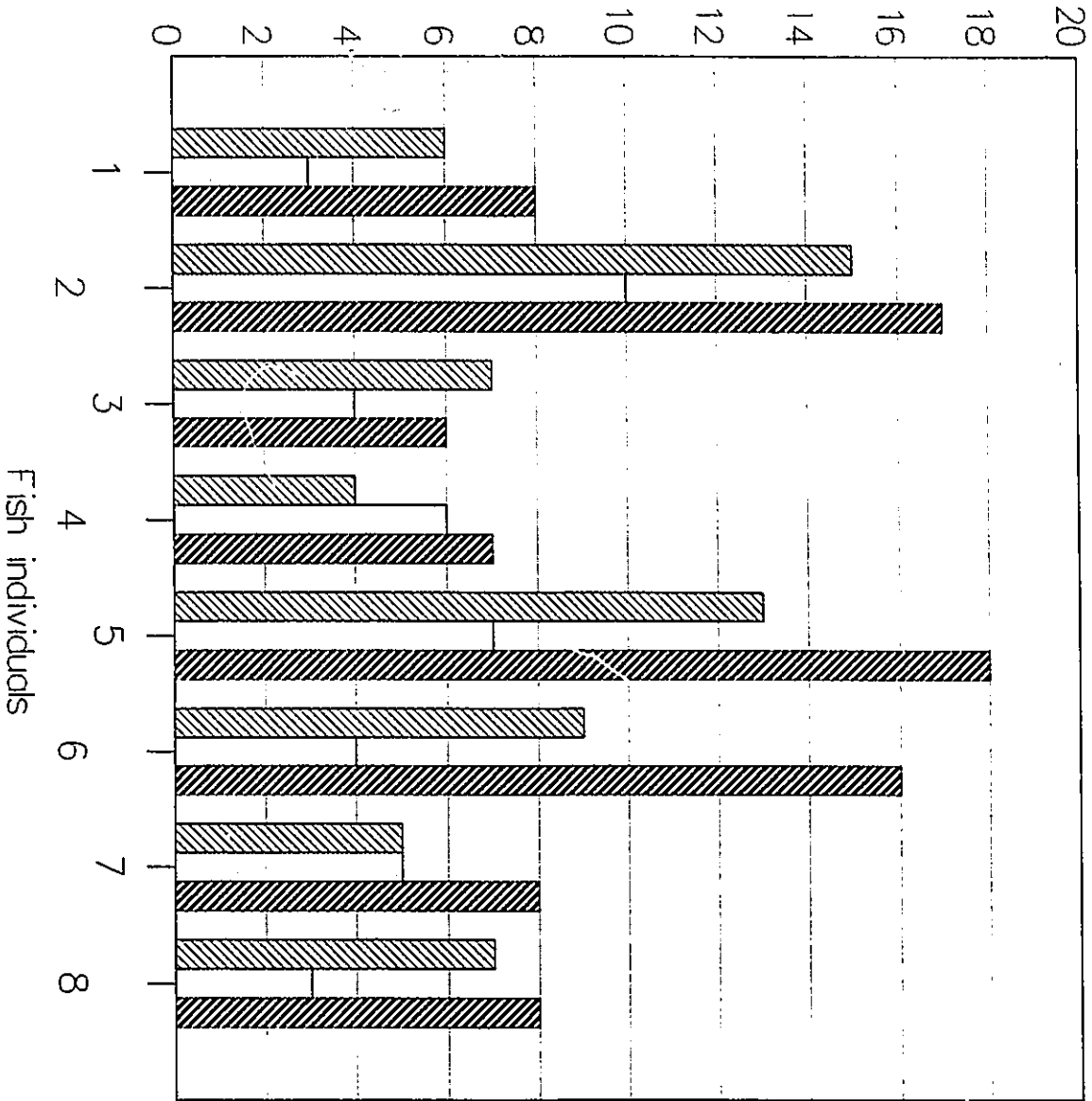


Figure. 6. Mean values for the number of regurgitations (%) made by eight individuals of pumpkinseed for Daphnia and Artemia and their mixture.

Regurgitations (%)

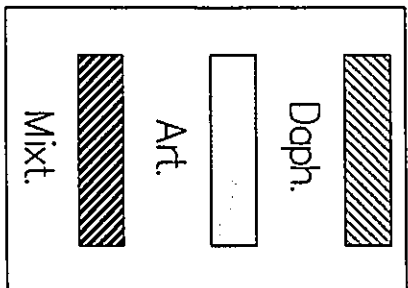
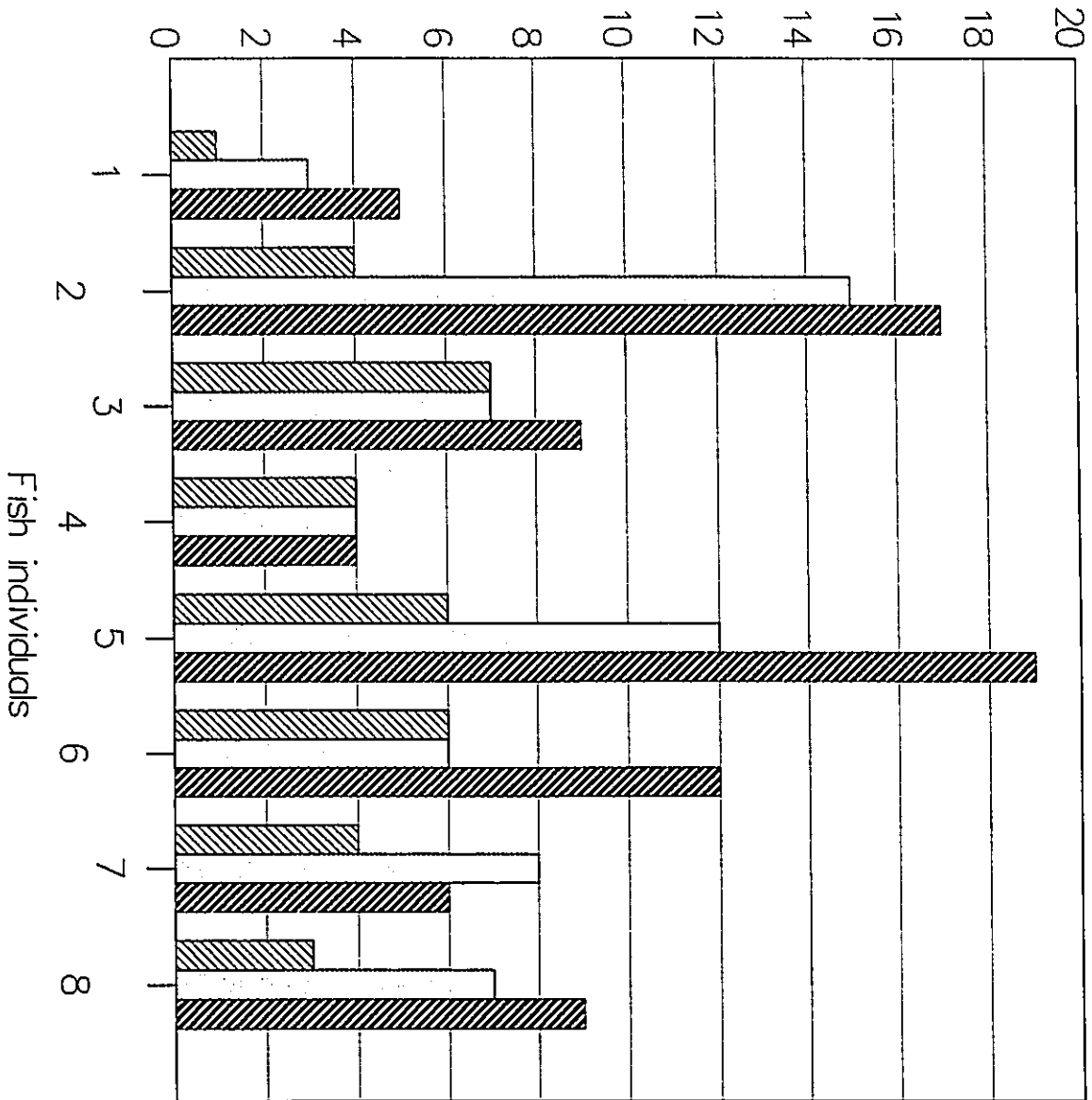


Figure 7. Mean values for time interval between feeding attempts in the beginning, middle and towards the end of the experiments for eight individuals of yellow perch for Daphnia and Artemia and their mixture.

Time interval (secs)

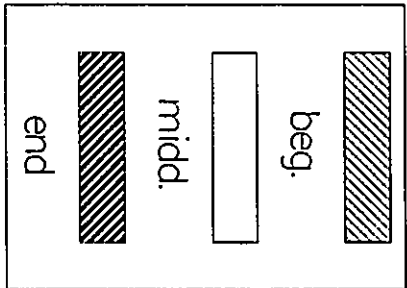
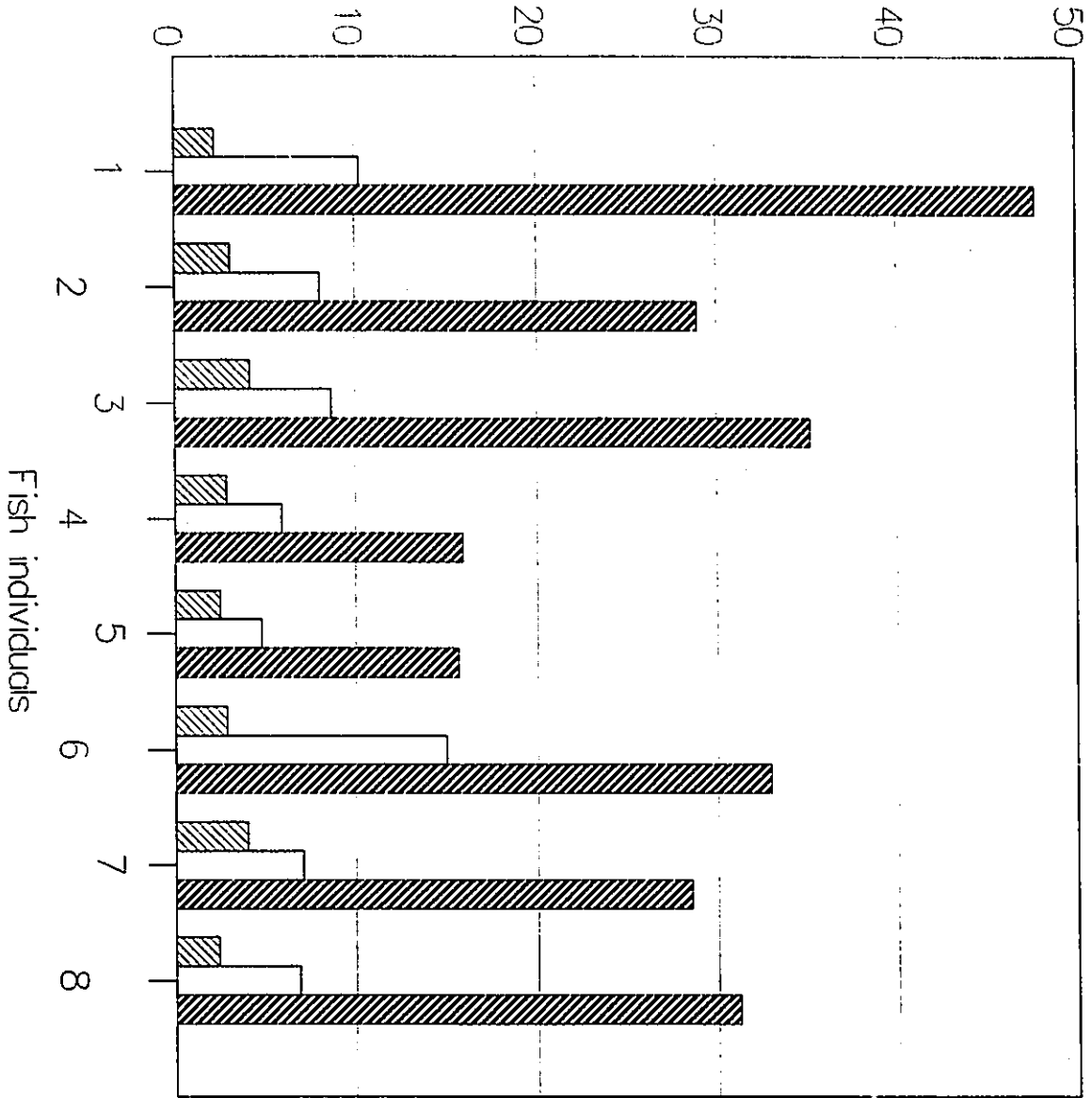


Figure 8. Mean values for total number of feeding attempts made by eight individuals of yellow perch for Daphnia and Artemia and their mixture.

Feeding attempts (No.)

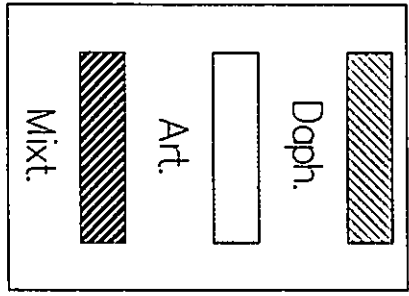
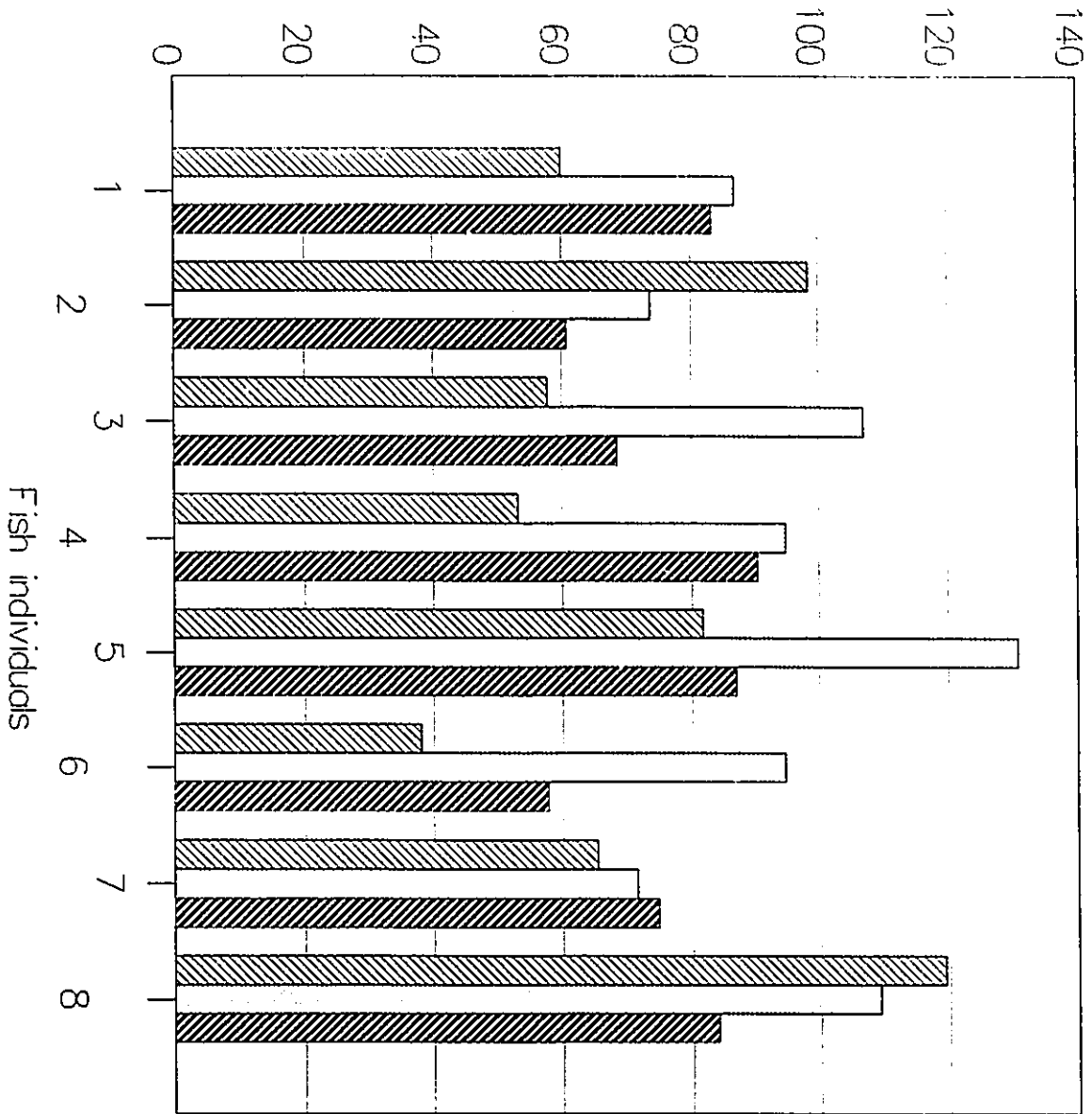


Figure 9. Mean values for number of unsuccessful attempts (%) made by eight individuals of yellow perch for Daphnia and Artemia and their mixture.

Unsuccessful attempts (%)

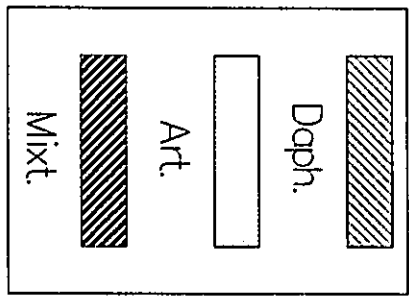
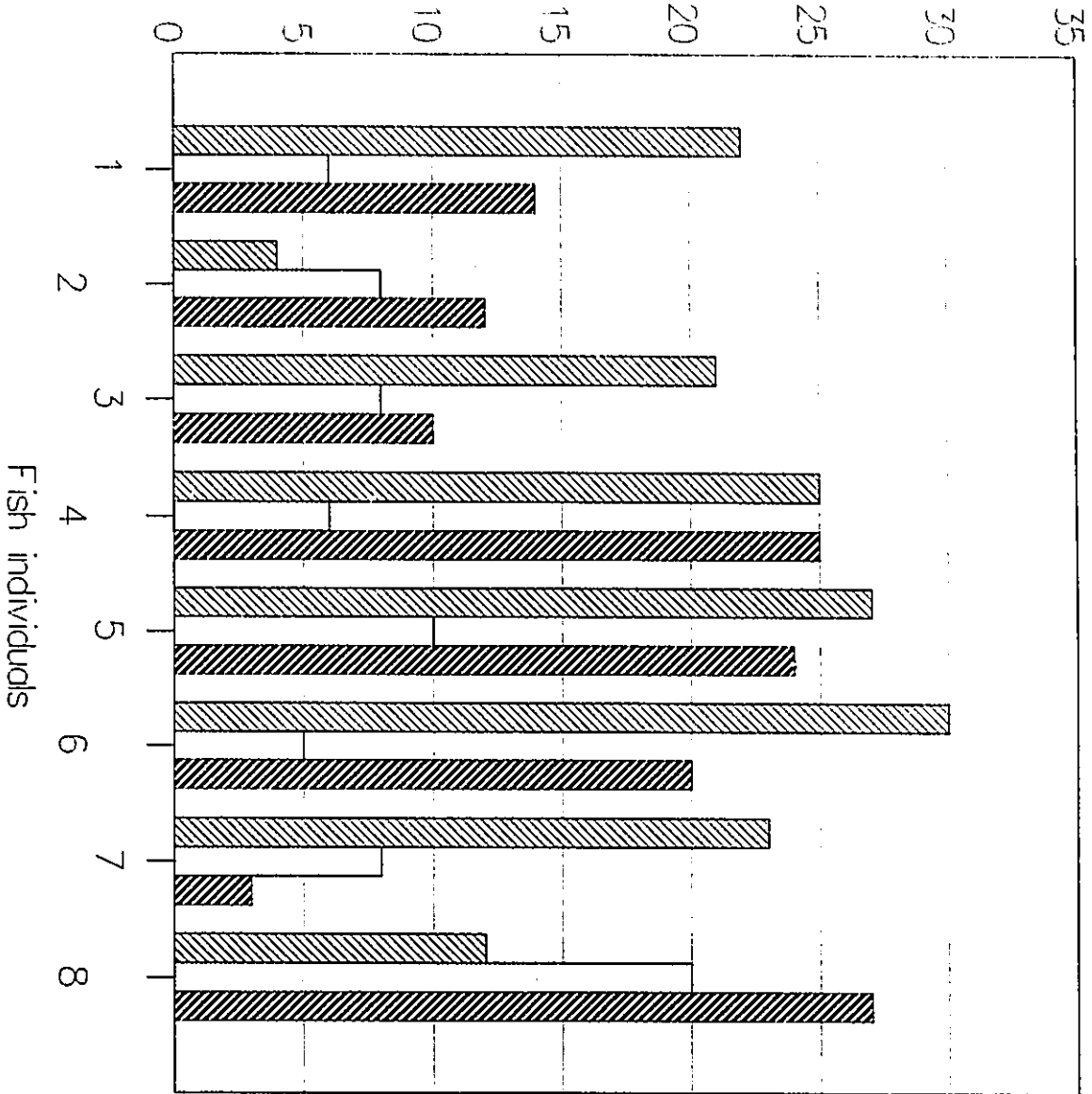
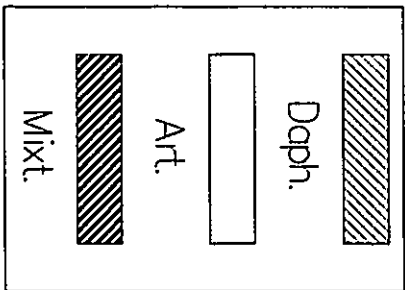
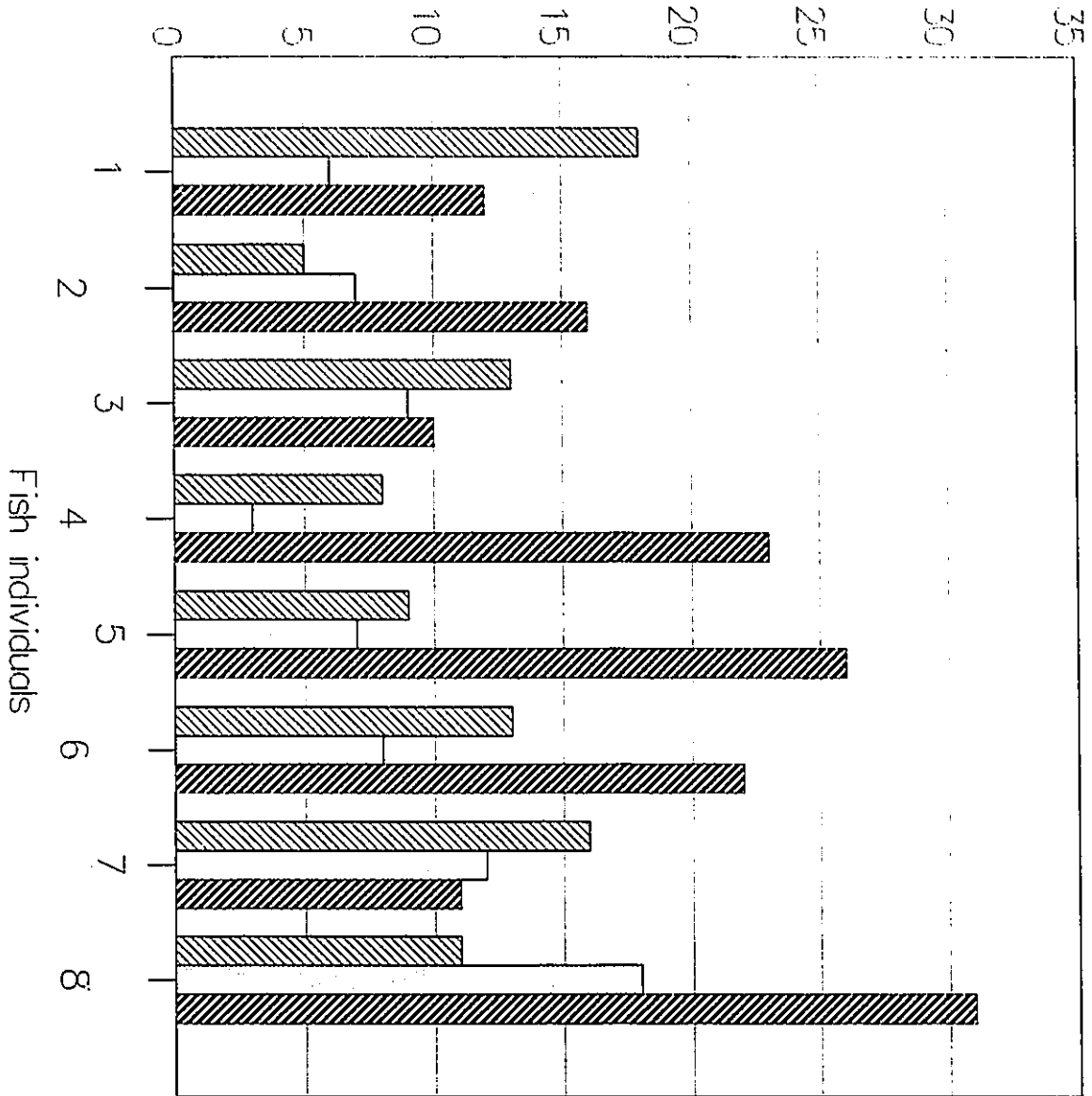


Figure 10. Mean values for the number of regurgitations (%) made by eight individuals of yellow perch for Daphnia and Artemia and their mixture.

Regurgitations (%)



4.2 Discussion

4.2.1 Pumpkinseed:

According to several ecologists, dissection of feeding behaviour into its component parts (such as encounter, attack rate, capture rate, and ingestion) provides information about the mechanism underlying prey selection (Holling 1966; Fedorenko 1975; Pastorok 1980; Milinski 1982; Greene 1983; Ringler 1983; Riensen et al. 1984; Wright and O'Brien 1984; Cooper et al. 1985). Individual variation among eight individuals for similar feeding variables was observed to provide an answer to the first question asked in the first chapter.

Individuals of young pumpkinseed differed much in all of the observed feeding variables. Time interval between feeding attempts and number of feeding attempts are important feeding variables and reflect information on prey detection, hunger and motivational state of animal (Cooper et al. 1985). An efficient forager can be expected to make fewer unsuccessful attempts and regurgitations.

Fish individuals did not differ much in the time intervals between feeding attempts in the beginning of the experiments, but large differences were observed at the middle and towards the end of the experiments (Fig. 2). This can be explained by the fact that the individuals were starved for 24h at the start of the experiment and may have fed voraciously. Higher predation rates by fish

individuals of sticklebacks at increased hunger (due to the low degree of satiation, more swimming activity and consequently a higher rate of prey encounter) were also observed by Beukema (1968), Ware (1972) and Kislalioglu and Gibson (1976). As they became more satiated, any individual differences in their abilities to perform and sustain their activities would become apparent. Ringler (1979) suggested that this phenomenon is important because it may regulate the rate of movements of different individuals among various food patches and, hence, the exploitation of various food resources by individuals. The individuals that get satiated early may not be able to exploit many food patches and may stop feeding earlier than others. Slater (1981) discussed a model explaining how two different foraging patterns are possible among conspecific individuals by small differences in their feeding rhythms. Results of this study clearly show that individuals of pumpkinseed differed in their foraging rhythms (Fig. 2).

The body angle at which a fish makes a feeding attempt has been considered important (Alexander 1967). Any variation in morphological characteristics, such as mouth shape, mouth position, buccal cavity and mouth size ratio and location of paired and median fins etc. can cause variation in the feeding angle among individuals. Most of the variation in the feeding angle occurred when fish were feeding on live Daphnia in mid-water column (Fig. 3). In the absence of data on the relevant morphological characteristics it is hard to explain these differences in the feeding angles in pumpkinseed sunfish. However, attacking live food

items in the mid- water column might require more accuracy in feeding angles since more unsuccessful attempts were made by the pumpkinseed individuals for live Daphnia (Fig. 5).

Exposing fish individuals to a diet composed of the mixture of Drosophila, Daphnia, and Artemia increased the percentage of unsuccessful attempts and regurgitations (Figs. 5 and 6). This might be due to the possibility that the presence of three types of food caused more confusion among individuals. Fish individuals might have spent more time in the selection of their preferred food type, as increased time interval between feeding attempts was observed for a mixed diet (Table 5). Individuals fed very little on Drosophila and that is why the time interval between feeding attempts for this food was high (Table 5).

Individuals of pumpkinseed differed in their frequency of feeding attempts (Fig. 4). The food finally captured by an individual may depend upon the number of feeding attempts, number of unsuccessful attempts and the number of regurgitations made in a feeding session. Individuals with more feeding attempts along with few unsuccessful attempts and regurgitations could be considered as more successful foragers. Figures 4, 5, and 6 show that individuals 2 and 5 made a high number of feeding attempts, more unsuccessful attempts and regurgitations. Individuals 4 and 7 also made high number of feeding attempts but with fewer unsuccessful attempts and regurgitations. The rest of the individuals were intermediate for the above feeding variables.

These results explain how the food capturing success among the conspecific individuals (e.g. number of captured food items) may differ depending on the individual's own ability to handle various food items. A large variation in the number of food items captured (30-277) was observed by McNicol et al. (1985) among young individuals (40-50 mm total length) of brook charr (Salvelinus fontinalis).

Variation among the individuals of different sexes were not examined. This study did not include the spawning or sexually mature individuals. Studies have suggested that differences in the feeding behaviour between the sexes of the same species occur only during the spawning season (Atmar and Stewart 1972; Cadwalladar 1975; Randolph and Clemens 1976; Ringler 1979; Ringler 1983).

4.2.2 Yellow perch:

As with the pumpkinseeds, individuals of yellow perch differed in their time intervals between feeding attempts, with most significant differences towards the end of the experiments (Table 6). Mean values for time intervals in the beginning, middle and towards the end of the experiments for eight individuals (Fig. 7) also showed that individuals had different feeding rhythms. Individuals 1 and 3 were active foragers only in the beginning and middle of the experiment but became more passive towards the end of the experiments. Individuals 4 and 5 fed actively at all phases of the experiments. Individuals 2 and 8 were generally passive.

Other individuals showed intermediate foraging rhythms.

Most of the perch individuals made the highest number of feeding attempts for Artemia. However, individuals 2 and 8 showed greater versatility than others by making more feeding attempts for Daphnia. Curio (1976) has also suggested that some individuals within a single species population may behave as generalists due to the greater within variation in their foraging strategies.

Individuals 2 and 8 made fewer unsuccessful attempts and regurgitations for Daphnia (Figs. 9 and 10) than others. These two individuals handled Daphnia better than Artemia, they also made highest number of feeding attempts for this food type. It shows that some individuals within a single species population may not only differ in their ability to forage on a particular food type but they may switch to a different food type showing a different food preference.

Figures 9 and 10 also showed that, similar to pumpkinseed when perch individuals were exposed to a mixture of Daphnia and Artemia the number of feeding attempts decreased and the percentage of unsuccessful attempts increased. This suggests the possibility that exposure of fish to a mixed diet leads to more confusion and time expenditure in the selection of preferred food type.

This study shows that individuals with differing foraging abilities are present within a single species population.

Individuals may vary from each other in their degree of activeness for various feeding variables. The foraging success of individuals may, however, depend upon a combination of such variables.

CHAPTER V

EFFECTS OF INCREASING POPULATION DENSITY ON THE INDIVIDUAL VARIATION IN THE FEEDING BEHAVIOUR OF PUMPKINSEED (LEPOMIS GIBBOSUS) AND YELLOW PERCH (PERCA FLAVESCENS)

5.1 Introduction

Some studies have been carried out to determine the effects of varying population density on the individual variation within a single species population. Rubenstein (1981) observed differences in the growth rates and reproductive potential of Everglades pygmy sunfish (*Elassoma evergladei*). These differences were magnified at high population densities of pygmy sunfish. The increase in the population density decreased the growth rate and reproductive potential of an average fish in the population. Some individuals in the same population, however, were only slightly affected.

Li and Brocksen (1977) examined the distribution of energetic relationships between a social hierarchy as density increased to determine the significance of dominance in relation to growth as a measure of fitness. They observed that the complexity of social interactions increased with population density and affected the growth patterns of each individual. However, the dominant individuals grew faster and were higher in fat content. The most submissive individuals stopped feeding mid-way and starved.

Far and Herrnkind (1974) found that the variance of courtship behaviour in *Poecillia reticulata* increased with density. Yamagishi (1962) and Yamagishi et al. (1974) observed that all the individuals in a population are not affected equally by the increased intensity of intraspecific competition and the dominant individuals always did better.

In spite of the above studies not much information is available on the effects of increasing population density on the feeding behaviour of conspecifics. This study found significant variation among individuals of pumpkinseed and yellow perch in their feeding patterns. This part of the project seeks answers to the following questions:

- i) is variation among conspecifics in their feeding behaviour affected by increasing population density ?
- ii) is the feeding behaviour of all the individuals in a population affected equally by the presence of other conspecifics ?

The above questions were investigated by analyzing the same feeding variables as described in chapter III but with different density and combinations of fish individuals (see below).

5.2 MATERIALS AND METHODS

Young specimens of pumpkinseed and yellow perch were obtained from Kettle Island Bay. Their size ranges and most of the experimental methods were the same as described in Chapter III. To study the effects of the increasing population density of conspecifics (intraspecific interactions) four individuals of pumpkinseed (P1, P2, P3, and P4) and yellow perch (Y1, Y2, Y3, and Y4) were used. The feeding behaviour of each individual was observed separately (to be used as control) and in groups of 2, 3, and 4 conspecifics in different combinations. These four individuals of each species were marked and kept in two separate

tanks which contained other five to seven individuals of the same species. The fish which were used to make different combinations and to increase the population density during the experiments were not always the same and were taken randomly from the holding tanks. The feeding behaviour of each individual was observed and compared with itself (in different combinations of other fish) and with other conspecific individuals (which were kept alone and with increasing population densities). This way it was possible to see that how the feeding behaviour of one individual is affected by the presence of other conspecifics, and how the variation among individuals is affected by increasing population density. The specific combinations used in this series of experiments are described in the tables of results. The analysis of variance and logit analysis were used to measure the effects of various combinations of conspecifics on the feeding behaviour of each individual and the variation among the four individuals of each species at different levels of increasing population densities.

For these experiments only two kinds of food, Daphnia and Artemia were used separately and in a mixture. The food density in the experiments increased (according to the total fish body weight) as the number of individuals increased to maintain a sufficient supply of food. The objective was to measure the effects of the presence of other conspecifics and increasing population density on the feeding behaviour of individuals. Similar to the last series each individual was tested three times for each food type at each level of increasing population density and combination of conspecifics.

5.3 Results

5.3.1 Effects of the presence of the conspecifics on the feeding behaviour

Analysis of variance and logit analysis showed that the feeding behaviour of each pumpkinseed and yellow perch was affected differently by the presence of other conspecifics in different combinations. Pumpkinseed P3 was the most affected individual by the presence of the other conspecific. For the time interval between feeding attempts in the beginning ($F=25.59$), middle ($F=28.34$), and towards the end ($F=35.88$) of the experiment (Table 8). All of these values were highly significant ($P<0.0001$). Logit analysis (Table 9) showed similar results for the number of unsuccessful feeding attempts ($\chi^2=53.26$, $P<0.0001$) and regurgitations ($\chi^2=96.29$, $P<0.0001$). Individual P4 was the least affected in terms of the above variables. The mean values of the four individuals for the above feeding variables showed similar results (Table 10).

Yellow perch individual Y2 showed the maximum variation for time interval between feeding attempts in the beginning ($F=12.19$, $P<0.0001$), in the middle ($F=28.29$, $P<0.0002$) and towards the end of the experiments ($F=26.24$, $P<0.0001$), number of unsuccessful feeding attempts ($\chi^2=32.77$, $P<0.0001$) and regurgitations ($\chi^2=55.04$, $P<0.0001$) for two types of food separately and in a mixture (Tables 11 and 12). Individual Y4 was the least affected individual in

terms of the above parameters. The mean values for all the four perch individuals for the above feeding variables and two types of food separately and in a mixture are given in Table 13.

5.3.2 Effects of increasing population density on the individual variation in the feeding behaviour among four individuals of pumpkinseed and yellow perch.

Results of analysis of variance and logit analysis for time interval between feeding attempts, number of unsuccessful attempts and regurgitations for four individuals of pumpkinseed and yellow perch are described in Tables 14, 15, 16, 17, 18 and 19.

As the number of individuals increased, the variation in feeding behaviour among individuals also increased. When pumpkinseed individuals P1, P2, P3, and P4 were examined separately the F values for time interval between feeding attempts in the beginning, middle and towards the end of the experiment were 1.10 ($P < 0.0911$), 1.20 ($P < 0.0923$) and 6.38 ($P < 0.006$), respectively. When the same individuals were observed in groups of four fish together, the F values for the above parameters increased to 11.73 ($P < 0.0001$), 24.16 ($P < 0.0001$) and 33.31 ($P < 0.0001$), respectively (Table 14). Similar patterns were observed for the number of unsuccessful attempts and regurgitations (Table 15).

Effects of increasing population density on the variation in feeding behaviour among four individuals of yellow perch were

Table 8. Effects of conspecifics on the feeding behaviour of four individuals of pumpkinseed for two types of food Daphnia and Artemia separately and in a mixture. Duration of each experiment was 10 minutes. Analysis of variance was used.

Combinations used	Time interval between feeding attempts in the beginning of experiments		Time interval between feeding attempts in the middle of experiments		Time interval between feeding attempts towards the end of the experiments	
	F	P<	F	P<	F	P<
P1						
P1+one fish	11.01	0.0001	25.12	0.0001	7.84	0.0001
P1+two fish	df=3, 207		df=3, 207		df=3, 192	
P1+three fish						
P2						
P2+one fish	7.63	0.0001	11.02	0.0001	2.54	0.0563
P2+two fish	df=3, 207		df=3, 207		df=3, 207	
P2+three fish						
P3						
P3+one fish	25.59	0.0001	28.34	0.0001	35.88	0.0001
P3+two fish	df=3, 208		df=3, 208		df=3, 197	
P3+three fish						
P4						
P4+one fish	2.37	0.0851	2.87	0.0881	1.22	0.308
P4+two fish	df=3, 197		df=3, 197		df=3, 193	
P4+three fish						

Table 9. Effects of conspecifics on the feeding behaviour of four individuals of pumpkinseed for two kinds of food Daphnia and Artemia separately and in a mixture. Duration of each experiment was 10 minutes. Logit analysis was used.

Combinations used	Number of unsuccessful attempts			Number of regurgitations		
	χ^2	df	P<	χ^2	df	P<
P1						
P1+one fish	37.06	3	0.0001	31.53	3	0.0001
P1+two fish						
P1+three fish						
P2						
P2+one fish	27.26	3	0.0001	23.14	3	0.0001
P2+two fish						
P2+three fish						
P3						
P3+one fish	53.26	3	0.0001	96.29	3	0.0001
P3+two fish						
P3+three fish						
P4						
P4+one fish	13.50	3	0.0587	11.65	3	0.0537
P4+two fish						
P4+three fish						

Table 10. Mean values for the feeding variables for four individuals of pumpkinseed (P1, P2, P3 and P4) alone and in the presence of other conspecifics. Two types of food Daphnia and Artemia were used separately and in a mixture. Duration of each experiment was 10 minutes.

Combinations used	Time interval between feeding attempts in the beginning of the experiments (Secs)	Time interval between feeding attempts in the middle of the experiments (Secs)	Time interval between feeding attempts towards the end of the experiments (Secs)	Number of unsuccessful feeding attempts	Number of regurgitations
P1+	2.67±0.35	8.20±5.95	33.99±18.73	4.44±2.54	4.66±2.44
P1+one fish	1.84±0.67	6.80±4.52	28.67±17.35	5.66±2.30	6.22±1.87
P1+two fish	2.64±1.35	6.41±5.28	22.80±12.22	23.22±7.53	7.11±2.23
P1+three fish	2.62±0.24	15.27±8.47	41.85±20.00	16.44±7.11	1.77±1.75
P2	2.43±0.50	4.51±3.08	20.58±16.36	12.22±4.36	5.88±2.13
P2+one fish	2.50±0.76	11.99±8.66	26.76±19.70	12.00±7.67	9.44±3.77
P2+two fish	2.45±0.57	7.89±6.82	21.69±16.30	11.00±3.12	15.55±2.58
P2+three fish	3.33±0.49	9.05±8.47	27.94±21.49	6.77±3.18	4.66±2.21
P3	1.22±0.87	5.93±1.66	15.88±3.29	6.36±1.49	7.12±4.80
P3+one fish	1.93±0.87	12.33±4.29	25.66±4.18	6.88±3.81	4.00±1.15
P3+two fish	1.99±0.24	15.39±3.22	33.66±12.73	9.12±4.16	12.75±11.1
P3+three fish	1.77±0.36	19.33±5.22	19.22±3.22	10.00±8.25	4.44±2.62
P4	1.22±0.67	4.22±0.92	29.11±11.23	10.33±7.85	8.55±4.54
P4+one fish	1.32±0.78	5.86±1.88	33.48±7.33	9.66±4.08	12.88±4.53
P4+two fish	1.24±0.11	7.33±1.62	27.66±6.22	11.11±4.74	7.11±2.23
P4+three fish	1.67±0.62	6.45±1.76	22.73±5.80	6.88±2.07	1.77±1.74

Means are followed by standard errors

Table 11. Effects of conspecifics on the feeding behaviour of four individuals of yellow perch for two types of food Daphnia and Artemia separately and in a mixture. Duration of each experiment was 10 minutes. Analysis of variance was used.

Combinations used	Time interval between feeding attempts in the beginning of experiments		Time interval between feeding attempts in the middle of experiments		Time interval between feeding attempts towards the end of the experiments	
	F	P<	F	P<	F	P<
Y1						
Y1+one fish	23.80	0.0001	10.66	0.0001	18.91	0.0001
Y1+two fish	df=3, 136		df=3, 136		df=3, 136	
Y1+three fish						
Y2						
Y2+one fish	12.19	0.0001	28.29	0.0002	26.24	0.0001
Y2+two fish	df=3, 136		df=3, 136		df=3, 136	
Y2+three fish						
Y3						
Y3+one fish	1.69	0.1795	13.62	0.014	10.85	0.0172
Y3+two fish	df=3, 136		df=3, 136		df=3, 136	
Y3+three fish						
Y4						
Y4+one fish	4.39	0.0081	2.34	0.0876	4.14	0.096
Y4+two fish	df=3, 136		df=3, 136		df=3, 136	
Y4+three fish						

Table 12. Effects of conspecifics on the feeding behaviour of four individuals of yellow perch for two types of food Daphnia and Artemia separately and in a mixture. Duration of each experiment was 10 minutes. Logit analysis was used.

Combinations used	Number of unsuccessful attempts			Number of regurgitations		
	χ^2	df	P<	χ^2	df	P<
Y1						
Y1+one fish	32.62	3	0.0001	15.91	3	0.0001
Y1+two fish						
Y1+three fish						
Y2						
Y2+one fish	32.77	3	0.0001	55.04	3	0.0001
Y2+two fish						
Y2+three fish						
Y3						
Y3+one fish	10.44	3	0.0244	9.85	3	0.0129
Y3+two fish						
Y3+three fish						
Y4						
Y4+one fish	10.08	3	0.0674	6.74	3	0.079
Y4+two fish						
Y4+three fish						

Table 13. Mean values for the feeding variables for four individuals of yellow perch (Y1, Y2, Y3 and Y4) alone and in the presence of other conspecifics. Two types of food *Daphnia* and *Artemia* were used separately and in a mixture. Duration of each experiment was 10 minutes.

combinations used	Time interval between feeding attempts in the beginning of the experiments (Secs)	Time interval between feeding attempts in the middle of the experiments (Secs)	Time interval between feeding attempts towards the end of the experiments (Secs)	Number of unsuccessful feeding attempts	Number of regurgitations
Y1	7.16±2.03	5.58±4.25	20.50±10.30	3.66±2.68	7.16±2.03
Y1+one fish	11.16±1.34	8.02±1.70	35.07±13.90	8.00±1.91	9.5±1.34
Y1+two fish	6.5±2.14	13.3±5.57	39.36±13.6	12.51±3.30	6.5±2.14
Y1+three fish	11.16±1.34	9.39±3.54	47.5±13.73	13.51±3.30	11.16±4.03
Y2	11.16±1.34	5.58±1.70	35.1±14.04	3.66±2.06	3.83±1.34
Y2+one fish	5.83±1.46	6.94±7.04	45.86±14.35	13.5±2.68	11.16±2.26
Y2+two fish	11.16±1.86	10.98±3.91	52.45±21.17	8.0±1.91	9.16±4.01
Y2+three fish	5.83±1.46	21.62±14.77	61.04±7.46	12.5±3.30	15.83±1.46
Y3	11.33±3.34	14.65±11.53	32.75±18.96	9.11±2.14	11.33±3.34
Y3+one fish	11.85±4.91	12.75±5.10	31.96±11.29	7.62±1.98	13.66±2.28
Y3+two fish	13.0±3.6	18.71±10.03	51.19±18.38	11.65±3.12	13.0±1.91
Y3+three fish	13.66±2.28	9.41±9.53	35.41±15.6	7.39±1.56	13.66±2.28
Y4	3.16±1.34	10.16±5.60	45.3±18.08	11.33±4.85	3.16±1.34
Y4+one fish	7.0±2.30	10.51±2.10	40.94±15.5	6.66±2.68	7.00±2.30
Y4+two fish	5.83±2.26	11.48±6.05	30.35±13.76	8.50±1.89	5.83±2.26
Y4+three fish	5.33±0.94	7.29±3.28	39.8±10.75	8.66±1.49	5.33±0.94

Means are followed by standard errors

Table 14. Variation in the feeding behaviour among the individuals of four pumpkinseed (P1, P2, P3 and P4) examined separately and in the combinations of increasing number of individuals. Two types of food Daphnia and Artemia were used. Duration of each experiment was 10 minutes. Analysis of variance was used.

Combinations used	Time interval between feeding attempts in the beginning of experiments		Time interval between feeding attempts in the middle of experiments		Time interval between feeding attempts towards the end of the experiments	
	F	P<	F	P<	F	P<
P1						
P2	1.10	0.0911	1.20	0.0923	6.38	0.0006
P3	df=3, 201		df=3, 201		df=3, 196	
P4						
Variance	18.31		43.72		1867.55	
P1+one fish						
P2+one fish	5.00	0.0001	9.10	0.0001	4.59	0.0076
P3+one fish	df=3, 198		df=3, 198		df=3, 190	
P4+one fish						
Variance	34.04		161.55		1263.87	
P1+two fish						
P2+two fish	10.09	0.8093	21.12	0.0001	15.10	0.0021
P3+two fish	df=3, 206		df=3, 206		df=3, 200	
P4+two fish						
Variance	88.57		1079.14		4015.45	
P1+three fish						
P2+three fish	11.73	0.0001	24.16	0.0001	33.31	0.0001
P3+three fish	df=3, 208		df=3, 208		df=3, 191	
P4+three fish						
Variance	223.35		1778.21		9294.63	

Variance among the fish individuals for each variable and population density is shown under the df values.

Table 15. Variation in the feeding behaviour among the individuals of four pumpkinseed (P1, P2, P3 and P4) examined separately and in the combinations of increasing number of individuals. Two types of food Daphnia and Artemia were used. Duration of each experiment was 10 minutes.

Logit analysis was used.

Combinations used	Number of unsuccessful attempts			Number of regurgitations		
	χ^2	df	P<	χ^2	df	P<
P1						
P2	10.45	3	0.0176	13.19	3	0.0044
P3						
P4						
P1+one fish						
P2+one fish	23.22	3	0.0007	14.03	3	0.0093
P3+one fish						
P4+one fish						
P1+two fish						
P2+two fish	45.79	3	0.0001	50.15	3	0.0001
P3+two fish						
P4+two fish						
P1+three fish						
P2+three fish	111.0	3	0.0001	83.07	3	0.0001
P3+three fish						
P4+three fish						

Table 16. Mean values for the feeding variables for four individuals of yellow perch (Y1, Y2, Y3 and Y4) examined separately and in the combinations of increasing number of individuals. Two types of food Daphnia and Artemia were used. Duration of each experiment was 10 minutes.

Combinations used	Time interval between feeding attempts in the beginning of the experiments (Secs)	Time interval between feeding attempts in the middle of the experiments (Secs)	Time interval between feeding attempts towards the end of the experiments (Secs)	Number of unsuccessful feeding attempts	Number of regurgitations
P1	2.54±1.33	6.80±5.08	22.55±17.99	4.14±2.53	14.77±10.6
P2	2.48±0.75	16.46±8.37	18.58±18.36	6.00±2.16	5.55±2.94
P3	2.39±0.95	9.33±8.56	29.52±11.08	4.37±3.56	7.37±3.23
P4	2.39±0.36	6.62±5.33	22.16±13.3	5.62±2.44	8.44±2.11
P1+one fish	1.88±0.67	6.72±4.50	28.49±17.58	7.70±3.80	9.66±4.00
P2+one fish	2.40±0.53	5.05±4.58	24.27±16.39	15.88±8.03	10.25±4.60
P3+one fish	3.26±0.25	8.51±7.01	21.42±18.3	6.22±3.76	4.66±1.56
P4+one fish	3.15±0.52	4.46±2.73	18.24±15.46	6.22±1.87	9.66±4.08
P1+two fish	2.67±0.35	8.20±5.95	22.35±18.56	5.99±2.22	5.44±2.54
P2+two fish	2.48±0.59	6.94±4.30	24.37±24.54	8.33±1.9	11.0±3.12
P3+two fish	2.66±0.90	5.73±3.33	33.84±16.80	12.92±2.63	9.12±4.16
P4+two fish	2.83±0.67	5.49±4.74	59.23±16.45	15.28±5.26	11.44±4.39
P1+three fish	2.62±0.24	15.16±8.66	39.86±20.4	9.44±4.64	20.88±4.97
P2+three fish	2.78±0.09	10.01±8.97	25.77±21.35	4.77±2.09	11.11±6.24
P3+three fish	2.09±0.52	7.26±5.44	25.31±5.41	15.25±2.81	15.55±2.49
P4+three fish	2.29±0.52	5.26±5.344	7.31±5.41	6.73±1.66	14.88±2.07

Means are followed by standard errors

Table 17. Variation in the feeding behaviour among the individuals of four yellow perch (Y1, Y2, Y3 and Y4) examined separately and in the combinations of increasing number of individuals. Two types of food Daphnia and Artemia were used. Duration of each experiment was 10 minutes. Analysis of variance was used.

Combinations used	Time interval between feeding attempts in the beginning of experiments		Time interval between feeding attempts in the middle of experiments		Time interval between feeding attempts towards the end of the experiments	
	F	P<	F	P<	F	P<
Y1						
Y2	8.24	0.0002	2.40	0.0621	4.45	0.007
Y3	df=3, 136		df=3, 136		df=3, 136	
Y4						
Variance	35.30		89.01		853.48	
Y1+one fish						
Y2+one fish	4.29	0.0085	4.63	0.0058	4.50	0.0066
Y3+one fish	df=3, 137		df=3, 137		df=3, 137	
Y4+one fish						
Variance	34.22		133.78		851.79	
Y1+two fish						
Y2+two fish	48.74	0.0001	16.75	0.0012	24.36	0.005
Y3+two fish	df=3, 136		df=3, 136		df=3, 136	
Y4+two fish						
Variance	1123.49		651.09		4874.04	
Y1+three fish						
Y2+three fish	70.62	0.0001	24.22	0.0009	31.17	0.0001
Y3+three fish	df=3, 145		df=3, 145		df=3, 145	
Y4+three fish						
Variance	2145.58		2110.90		5473.13	

Variance among the fish individuals for each variable and population density is shown under the df values.

Table 18. Variation in the feeding behaviour among the individuals of four yellow perch (Y1, Y2, Y3 and Y4) examined separately and in the combinations of increasing number of individuals. Two types of food Daphnia and Artemia were used. Duration of each experiment was 10 minutes.

Logit analysis was used.

Combinations used	Number of unsuccessful attempts			Number of regurgitations		
	χ^2	df	P<	χ^2	df	P<
Y1						
Y2	14.75	3	0.0025	8.27	3	0.0315
Y3						
Y4						
Y1+one fish						
Y2+one fish	18.96	3	0.0004	14.21	3	0.0025
Y3+one fish						
Y4+one fish						
Y1+two fish						
Y2+two fish	40.09	3	0.0001	46.37	3	0.0001
Y3+two fish						
Y4+two fish						
Y1+three fish						
Y2+three fish	71.10	3	0.0001	124.91	3	0.0001
Y3+three fish						
Y4+three fish						

Table 19. Mean values for the feeding variables for four individuals of yellow perch (Y1, Y2, Y3 and Y4) examined separately and in the combinations of increasing number of individuals. Two types of food Daphnia and Artemia were used. Duration of each experiment was 10 minutes.

combinations used	Time interval between feeding attempts in the beginning of the experiments (Secs)	Time interval between feeding attempts in the middle of the experiments (Secs)	Time interval between feeding attempts towards the end of the experiments (Secs)	Number of unsuccessful feeding attempts	Number of regurgitations
Y1	2.92±1.92	8.35±4.09	20.50±10.30	9.83±3.67	7.16±2.03
Y2	12.55±0.63	14.80±8.48	34.56±18.9	10.83±1.67	10.13±1.5
Y3	1.16±0.42	14.65±11.53	32.72±18.96	12.14±2.74	11.33±3.34
Y4	3.30±2.13	9.23±5.16	43.30±19.35	11.2±2.48	20.57±13.69
Y1+one fish	1.88±0.37	5.58±1.70	35.07±13.99	13.83±5.04	7.16±2.03
Y2+one fish	1.11±0.53	10.98±7.04	52.87±14.35	6.50±3.30	11.25±1.34
Y3+one fish	2.46±1.30	12.73±4.90	34.46±13.89	5.66±1.88	11.33±3.34
Y4+one fish	0.76±0.29	12.41±8.72	38.73±16.28	13.33±9.04	18.16±13.35
Y1+two fish	0.7±0.36	6.91±0.36	39.36±1.36	13.50±2.06	11.16±2.74
Y2+two fish	3.81±1.29	13.61±3.85	45.87±21.18	3.66±2.68	2.83±2.26
Y3+two fish	0.83±0.48	18.32±9.73	51.19±18.38	11.50±2.43	13.66±2.28
Y4+two fish	3.65±1.02	11.82±7.62	25.55±7.37	3.66±2.68	3.83±2.26
Y1+three fish	1.11±0.62	7.29±3.70	47.5±13.73	12.16±1.95	19.50±4.03
Y2+three fish	1.75±0.48	21.55±14.66	61.04±7.46	15.16±5.45	15.83±1.46
Y3+three fish	1.76±0.67	13.50±11.86	43.85±5.31	5.33±2.74	11.66±2.28
Y4+three fish	5.36±1.04	11.30±3.28	29.77±10.29	2.16±0.68	5.33±0.94

Means are followed by standard errors

similar to pumpkinseed. Results of the analysis of variance showed that when four individuals were examined separately the F values for time interval between feeding attempts in the beginning, middle and towards the end of the experiments were 8.24 ($P < 0.0001$), 2.40 ($P < 0.0621$) and 4.45 ($P < 0.0070$), respectively. When the number of individuals in the experiments was increased to four, the F values increased to 70.62 ($P < 0.0001$), 24.22 ($P < 0.0009$) and 31.17 ($P < 0.0001$), respectively (Table 17). Similar results were obtained for the number of unsuccessful attempts and regurgitations (Table 18). The mean values for the above feeding variables for four individuals of pumpkinseed and yellow perch are given in Table 16 and 19.

The values of the variance for pumpkinseed (Table 14) and yellow perch (Table 17) show that the variation among fish increased, when population density increased. This increase in the variance was observed most of the times for individuals of both the species.

Discussion

Results of this study clearly show that individuals of pumpkinseed and yellow perch are not equally affected in the presence of other conspecifics. The feeding behaviour of P3 among the four individuals of pumpkinseed showed highest variation by the presence of other conspecifics (Tables 8 and 9). We can expect this individual to be very submissive in its environment. Individual P4

was the least-affected individual in the presence of other conspecifics for its feeding behaviour. This individual can be expected to forage more successfully than others because it can sustain its feeding even in the presence of other individuals.

Similar results were obtained for the individuals of yellow perch. Individual Y4 was the least affected, and individual Y2 was the most affected individual of yellow perch.

The presence of such a distinct and significant variation among individuals suggests that focusing on individuals may provide deeper insight into the structure of biological communities, particularly in guilds (Roots 1967) where variation in individual's abilities irrespective of species might be more important in determining the interspecific interactions than are average taxonomic differences, or in the tropics where population densities per species are low but the number of species is high (Wilbur 1976).

Differential predation on animals varying in their abilities might have dramatic effects on the dynamics of a population and its place in the community. If a predator concentrated its attacks on the largest, fastest and most efficient individuals of the population, the ecological implications might be very different than if the predator concentrated its attack on the smaller, weaker and less efficient members of the population. If predation eliminated the best individuals, those most efficient at utilizing the resources and converting energy into offspring, than the newly

released resources might not be efficiently used by the remaining individuals which were the poorer exploiters. If some of the resources are lost to other species then the whole structure of the community will be altered.

These experiments were designed to examine the biological realism of some of the assumptions underlying the simple models of population dynamics and to determine whether ignoring the implications of these assumptions limits our understanding of intra- and interspecific interactions. The results clearly show that the assumption of equal competitive ability may not be true as in our experiments some individuals were not affected significantly by the presence of conspecifics. Individuals showed inherent variability in their ability to exploit various food resources and to interact with each other. And this variability increased significantly when the population density of each species was increased. An increased number of individuals in the experiments magnified the variation among individuals of both the species. Though our results could be biased to some extent as the fish which were used to increase the population density in the experiment were not always the same. However, the increase of variance among individuals along with the increasing population density suggests that an increased population density may magnify the differences among individuals. Similar results for the density induced variation in individual growth rate and survival have been found in pygmy sunfish (Rubenstein 1981), green sunfish (Allee et al. 1948), rainbow trout (Li and Brocksen 1977) blowfly larvae (Nicholson 1954) and a variety of species of amphibian larvae (Rose

1960; Wilbur 1976, 1977; Steinwascher 1978). Thus the phenomenon is wide-spread. In this study the same patterns were observed at the level of food utilization behaviour quantitatively, which may ultimately affect the growth patterns among fishes, as many of the fish populations are food limited.

Our results show that ignoring the differences between individuals of a single species population may easily distort our understanding of various interactions within and between the species. Increasing density may result into an average decrease in the ability of food exploitation, but focusing on averages obscures the fact that the abilities of some individuals may not be affected at all by the presence of other individuals. The results of this study suggest that ecologists should also focus on individuals. This can be done in part by describing populations not only in terms of size and average responses, but in terms of variance and skewness as well. If ecologists are to evaluate fully the consequences of individual variation on the dynamics of populations and communities, the role of individual variation in intra- and interspecific interactions must be incorporated into ecological theories and models.

CHAPTER VI
FEEDING INTERACTIONS
BETWEEN PUMPKINSEED
(LEPOMIS GIBBOSUS) AND
YELLOW PERCH (PERCA
FLAVESCENS)

6.1 Introduction

Studies on the intra- and interspecific feeding interactions have been done by measuring the niche overlap (Mendelson 1975; Marrin and Erman 1982; Gladfelter and Johnson 1983; McCabe et al. 1984), or by comparative studies testing for diet shifts in fish species which occur sympatrically and allopatrically (Andrusak and Northcote 1971; Nilsson and Northcote 1981; Magnan and Fitzgerald 1982; Schemit and Coyer 1983). Some experimental studies have also been made to observe the effects of competitive interactions on the utilization of food resources among fish species (Werner and Hall 1976, 1977, 1979; Robertson et al. 1976; Faush and white 1981; Larson 1980). Studies such as these often have problems because factors such as the effects of competition, changes in the prey abundance and the availability, or the structural differences between the habitats are hard to identify and segregate from each other. Most of the field experiments done in the past have used the stocking densities that were not close to the natural densities. Such problems can limit the insight gained (Maiorana 1977; Schoener 1983; Hanson and Leggett 1985, 1986). Therefore, discrepancies in the results of field experiments have often been observed when the proper (close to the natural) stocking densities were used (Clady and Luker 1982). Measuring the natural density of fish without disturbing the environment itself is a very difficult task.

Another way of looking at such interactions closely is to perform well designed laboratory experiments. This way the

manipulation of only those variables is possible which are specifically under question. In this study it assumed that the feeding behaviour of fishes at the level at which their basic abilities are concerned would not change significantly in the field qualitatively. This assumption is based on several studies such as Kelleberg (1958), Vascotto and Morrow (1973), McNicol and Noaks (1984), McNicol et al. (1985) and Dill et al. (1981). These studies have been done simultaneously in the field and laboratory showing that when behavioral activities are observed in the field and in the laboratory, their nature and the proportion of various activities do not change substantially. For example McNicol et al. (1985) observed that the behavioral activities of the young of the year of brook charr Salvelinus fontinalis, such as how an individual occupies a position in the territory, its feeding or reproduction, agonistic interactions with other conspecifics or the heterospecifics decreased quantitatively in the field. However, the proportion of various activities and their basic nature was the same. In this last series of experiments we examined the effects of heterospecifics on the feeding behaviour of individual pumpkinseed. Combinations with conspecifics were also used to compare the effects of intra and interspecific interactions. This provides answer to our last question, are all the individuals of pumpkinseed and yellow perch affected equally during the intra- and interspecific interactions?

6.2. Materials and methods

Methodologies used for this last series of experiments were the same as in our earlier experiments except that the species were mixed. The experiments were performed in a random order again for two kinds of food Daphnia and Artemia, separately and in a mixture. To compare the effects of intra- and interspecific interactions combinations of one and two specimens of pumpkinseed and yellow perch (shown in the tables of the results of this chapter) were used. Two individuals of pumpkinseed and two individuals of yellow perch were selected for this study and were tested for their feeding behaviour in the presence of an increasing number of conspecifics and heterospecifics (perch for pumpkinseed and pumpkinseed for yellow perch). Fish that was used to make combinations of increasing densities of conspecifics and heterospecifics were not always the same and were selected randomly from two holding tanks which contained approximately seven fish.

6.3. Results

Data for various combinations of pumpkinseed and yellow perch were analyzed for two types of food Daphnia and Artemia separately and in a mixture. When the effects of intra- and interspecific interactions were observed on the individuals of pumpkinseed using only two fish in the experiments (conspecific or heterospecific), significant effects were observed only in the presence of conspecifics (for individual P1 Table 20 for the number of

Table 20. Effects of conspecifics and heterospecifics on the feeding behaviour of pumpkinseed P1 for two kinds of food Daphnia and Artemia separately and in a mixture. Duration of each experiment was 10 minutes. Logit analysis was used

Combinations used	Number of unsuccessful attempts			Number of regurgitiations		
	χ^2	df	P<	χ^2	df	P<
p1						
p1+one P.seed	5.75	1	0.0102	12.62	1	0.0102
P1						
P1+one perch	4.92	1	0.0646	1.41	1	0.0647
P1						
P1+two P.seed	22.47	1	0.0559	5.62	1	0.0153
P1						
P1+two perch	2.07	1	0.0669	2.24	1	0.1370
P1						
P1+three P.seed	31.66	1	0.0001	25.12	1	0.0001
P1						
P1+three perch	11.39	1	0.0043	8.37	1	0.0009

* feeding behaviour of these individuals were compared

Table 21. Effects of conspecifics and heterospecifics on the feeding behaviour of pumpkinseed p1 for two types of food Daphnia and Artemia separately and in a mixture. Duration of each experiment was 10 minutes. Analysis of variance was used.

Combinations used	Time interval between feeding attempts in the beginning of experiments		Time interval between feeding attempts in the middle of experiments		Time interval between feeding attempts towards the end of the experiments	
	F	P<	F	P<	F	P<
P1 P1+one P.seed	17.34 df=1, 67	0.0001	36.42 df=1, 67	0.0001	17.94 df=1, 67	0.0001
P1 P1+one perch	12.85 df=1, 66	0.0907	4.90 df=1, 66	0.0350	0.01 df=1, 66	0.7670
P1 P1+two P.seed	15.38 df=1, 66	0.0002	28.21 df=1, 66	0.0001	9.42 df=1, 66	0.0032
P1 P1+two perch	14.96 df=1, 66	0.0003	5.92 df=1, 66	0.0001	2.43 df=1, 66	0.0993
P1 P1+three P.seed	17.58 df=1, 66	0.0001	70.17 df=1, 66	0.0001	44.35 df=1, 66	0.0001
P1 P1+three perch	8.08 df=1, 66	0.0057	15.21 df=1, 66	0.0002	12.55 df=1, 66	0.0006

Table 22. Effects of conspecifics and heterospecifics on the feeding behaviour of pumpkinseed P2 for two kinds of food Daphnia and Artemia separately and in a mixture. Duration of each experiment was 10 minutes. Logit analysis was used

Combinations used	Number of unsuccessful attempts			Number of regurgitations		
	χ^2	df	P<	χ^2	df	P<
p2						
p2+one P.seed	14.05	1	0.0001	33.38	1	0.0001
P2						
P2+one perch	0.12	1	0.7682	1.57	1	0.218
P2						
P2+two P.seed	18.87	1	0.0001	5.67	1	0.0158
P2						
P2+two perch	3.40	1	0.0566	3.59	1	0.0529
P2						
P2+three P.seed	50.82	1	0.0001	51.65	1	0.0001
P2						
P2+three perch	20.06	1	0.0001	48.12	1	0.0001

Table 23. Effects of conspecifics and heterospecifics on the feeding behaviour of pumpkinseed p2 for two types of food Daphnia and Artemia separately and in a mixture. Duration of each experiment was 10 minutes. Analysis of variance was used.

Combinations used	Time interval between feeding attempts in the beginning of experiments		Time interval between feeding attempts in the middle of experiments		Time interval between feeding attempts towards the end of the experiments	
	F	P<	F	P<	F	P<
P2 P2+one P.seed	8.29 df=1, 66	0.0060	17.18 df=1, 66	0.0001	7.87 df=1, 66	0.0078
P2 P2+one perch	0.50 df=1, 66	0.4198	9.31 df=1, 66	0.0028	2.78 df=1, 66	0.3704
P2 P2+two P.seed	15.15 df=1, 66	0.0003	50.39 df=1, 66	0.0001	29.73 df=1, 66	0.0001
P21 P2+two perch	7.65 df=1, 66	0.0083	17.92 df=1, 66	0.0001	0.31 df=1, 66	0.6051
P2 P2+three P.seed	21.78 df=1, 66	0.0001	72.34 df=1, 66	0.0001	71.38 df=1, 66	0.0001
P2 P2+three perch	11.24 df=1, 66	0.0258	40.01 df=1, 66	0.0001	36.70 df=1, 66	0.0001

Table 24. Mean values for the feeding variables examined for pumpkinseed individual (P1) alone and in combinations of other conspecifics and heterospecifics (yellow perch). Two types of food Daphnia and Artemia were used separately and in a mixture. Duration of each experiment was 10 minutes.

combinations used	time interval between feeding attempts in the beginning of the experiments (Secs)	time interval between feeding attempts in the middle of the experiments (Secs)	time interval between feeding attempts towards the end of the experiments (Secs)	number of unsuccessful feeding attempts	number of regurgitations
P1	2.03±0.57	9.82±3.87	35.44±11.25	5.55±2.92	6.66±3.19
P1+one p.seed	4.33±1.28	4.31±2.19	17.58±9.62	8.33±1.97	11.66±3.19
P1	1.95±0.91	6.28±3.52	19.88±7.33	5.55±2.92	6.66±3.44
P1+one perch	3.51±1.69	4.35±1.17	17.16±7.40	13.33±5.08	17.00±3.10
P1	1.76±0.57	8.79±4.19	30.78±14.33	5.55±2.92	6.66±3.44
P1+two p.seed	2.89±1.10	3.90±1.78	14.08±1.78	8.83±4.25	5.16±2.67
P1	1.70±0.48	6.40±2.28	27.39±14.90	5.55±2.92	6.66±3.44
P1+two perch	2.74±1.11	3.95±2.74	15.98±5.48	26.28±5.26	12.16±2.67
P1	3.74±1.73	12.78±6.68	45.9±11.46	5.55±2.92	6.66±3.44
P1+three p.seed	2.87±1.20	4.34±3.34	16.47±5.60	9.66±5.43	12.00±3.39
P1	2.46±1.15	7.88±2.31	34.40±12.08	5.55±2.92	6.66±3.44
P1+three perch	2.83±1.18	6.95±1.74	16.09±5.17	16.00±3.46	11.50±2.56

Means are followed by standard errors

Table 25. Mean values for the feeding variables examined for pumpkinseed individual (P2) alone and in combinations of other conspecifics and heterospecifics (yellow perch). Two types of food Daphnia and Artemia were used separately and in a mixture. Duration of each experiment was 10 minutes.

combinations used	time interval between feeding attempts in the beginning of the experiments (Secs)	time interval between feeding attempts in the middle of the experiments (Secs)	time interval between feeding attempts towards the end of the experiments (Secs)	number of unsuccessful feeding attempts	number of regurgitations
P2	2.62±1.71	6.20±3.42	26.50±6.29	14.66±7.79	23.46±4.87
P2+one p.seed	2.50±1.41	9.44±4.54	37.97±14.39	12.50±4.07	13.25±3.78
P2	1.12±0.89	6.67±2.83	36.08±8.95	14.66±7.79	13.87±2.76
P2+one perch	2.21±1.04	9.30±3.42	22.84±6.16	21.83±9.50	15.00±5.44
P2	2.62±1.11	6.17±2.41	27.61±6.21	14.66±7.79	19.31±5.44
P2+two p.seed	2.07±1.02	10.68±4.77	25.30±9.54	10.50±5.82	10.16±5.44
P2	2.57±1.66	18.09±4.29	26.06±5.95	14.66±7.79	12.66±1.93
P2+two perch	4.46±1.11	13.09±4.29	49.71±16.13	17.00±9.80	13.50±3.86
P2	2.59±1.12	6.25±1.35	36.05±6.20	14.66±7.79	17.68±3.56
P2+three p.seed	2.07±0.86	10.53±3.72	48.64±9.01	6.16±1.06	10.16±3.28
P2	2.58±1.69	6.24±2.34	26.07±6.21	14.66±7.79	7.66±2.56
P2+three perch	4.17±1.06	16.16±5.37	42.37±14.83	18.33±7.58	10.66±3.58

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Means are followed by standard errors

unsuccessful attempts and regurgitations and Table 21 for the time interval between the feeding attempts in the beginning, middle and towards the end of the experiments). Similar effects were observed for individual P2 (Tables 22 and 23). These analyses also showed that for both the individuals of pumpkinseed the overall effects of conspecifics were greater than heterospecifics (i.e. of yellow perch). However, Tables 20, 21, 22 and 23 showed that when the density of heterospecifics increased in the experiments, their effects also increased proportionally but not to the same extent as for conspecifics. Tables 20, 21, 22 and 23 also show that for the time interval between feeding attempts in the beginning, middle and towards the end of experiments the effects of conspecifics were much greater than the effects of heterospecifics at the lowest experimental density. At higher density, however, there was not much difference between the effects of conspecifics and heterospecifics. Results also showed that pumpkinseed individual P2 was more affected than P1. Mean values for the above feeding variables for pumpkinseed P1 and P2 in the presence of conspecifics and heterospecifics are shown in Tables 24 and 25.

6.4. Discussion

Results of this study demonstrate some effects of intra- and interspecific interactions on the feeding behaviour of pumpkinseed. Outcome of this study supports the results of Hanson and Leggett (1985), who performed field experiments to investigate the competitive interactions within and between pumpkinseed and yellow

perch in Lake Memphremogog. Their study showed that the effects of conspecifics on the feeding behaviour of both the species increased as the population density increased. Effects of yellow perch on the feeding behaviour of pumpkinseed were small at a lower density as compared to the effects of conspecifics. But at a higher density the effects of the yellow perch increased substantially. They suggested that among pumpkinseed and yellow perch the former was a superior species.

Our results indicated that the effects of the intra- and interspecific interactions were not equal on both the individuals of pumpkinseed. Individual P2 was more affected than P1. It shows how concentrating our attention only on the averages can give us incomplete information regarding the nature of such interactions. Other researchers have also stressed that we should not assume the equal competitive abilities of all individuals in a population specially when studying the interaction between two or more species (Weins 1973, 1976; Weins and Dyer 1975; Magurran 1976 and Rubenstein 1981).

Results of this study also indicated that the nature and the intensity of interactions between the two species changes with the size of interacting populations. For example, at a low population density the effects of yellow perch on pumpkinseed individuals were not significant but as the population density increased effects became significant. This also suggest that to predict the effects of various interactions within and between the species the

knowledge of proportional abundance of interacting species is also very important. this was also observed by Persson (1983).

Results of the studies done by Hanson and Leggett (1985, 1986) on the competitive interactions within and between yellow perch and pumpkinseed showed that only interspecific interactions may cause changes in the kinds of the diets of the species and force them to include the food items of less energetic values in their diets. The intraspecific interactions would cause only a general decrease in the amount of food eaten by all the individuals. This explanation was based on the assumption that all the individuals in a population are similar in their foraging efficiencies and when the resource abundance decreases in the environment all the conspecifics are equally affected. On the other hand, this study shows that some individuals in a population are superior in their foraging abilities than others and are little or less affected during the intra- and interspecific interactions. So the increased niche breadth of a population could also be a result of intraspecific interactions (Christiansen and Fenchel 1977; Pianka 1978 and Svardson 1949). The results of this study show that only the weaker individuals of a species are more likely to be affected during the intra- or interspecific interactions.

Studies such as MacArthur and Pianka (1966) have suggested that an animal should not change its diet in a habitat due the presence of a competitor but rather should spend less time in that habitat. This switch in the habitat should be due to the depletion

of food resources (exploitative interaction). However, our study (chapter IV) showed that different species have different foraging abilities and preference for different food items. Therefore, the major reason for avoiding an overlap in the use of a particular habitat could be interference type of interaction. As this study showed that even the presence of conspecifics or heterospecifics may affect the foraging efficiency of an individual. The intensity of this interference type of interactions should be greater in lakes and ponds (an aquarium like situation) where all the species generally use most of the available habitats (Keast 1977; Hall and Werner 1977). In the laboratory studies the intensity of such interactions could be higher because a smaller area was available to fishes in the aquarium as compared to the natural environments. But the results might not change qualitatively as they were quite comparable to other studies which were done in the natural environments.

CONCLUSIONS

Individuals of pumpkinseed and yellow perch differed significantly in their food handling abilities (ability to make feeding attempts, time interval between feeding attempts in the beginning, middle and towards the end of the experiments, feeding angle, number of unsuccessful attempts and regurgitations) tested against three kinds of food Drosophila, Daphnia and Artemia separately and in a mixture. Altogether groups of conspecifics with different foraging patterns were identified. Some individuals were active, some were passive and some were intermediate in their feeding activities. The results of this study clearly showed that the assumption of equal competitive abilities of the individuals of a single species was not true.

This study further showed that individuals of pumpkinseed and yellow perch were not equally affected in the presence of other conspecifics. There was inherent variability among individuals in their ability to exploit various food resources and to affect the feeding behaviour of each other. This variation was magnified when the population density of both the species was increased. So the assumption by many ecologist that the competitive ability of an average individual is not affected by the density of the population did not hold true in this case.

Pumpkinseed individuals were superior in their foraging ability to the individuals of yellow perch. During the feeding interactions between the individuals of pumpkinseed and yellow perch the feeding behaviour of all the individuals of pumpkinseed was not affected equally. The nature and the intensity of feeding interactions between the two species changed with the density of the populations included in the interactions. At low population density the effects of yellow perch on pumpkinseed individuals were not significant, as the population density increased the effects became pronounced.

It was suggested that ignoring the differences between individuals of a single species population could easily distort our understanding of interactions within and between the species. Ecologist should also focus their attention on the individuals, and the role of individual variation in intra and interspecific interactions must be incorporated into our ecological models and theories.

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