Behav Ecol Sociobiol (1986) 19:373–379

Behavioral Ecology and Sociobiology

Individual and species recognition in centrarchid fishes: evidence and hypotheses

Joseph A. Brown[1] **and Patrick W. Colgan**[2]

[1] Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Nfld., Canada A1C 5S7
[2] Department of Biology, Queen's University, Kingston, Ontario, Canada K7N 3N6

Received January 29, 1986 / Accepted June 7, 1986

Summary. We conducted laboratory experiments to determine if juveniles of three species of centrarchid fishes displayed abilities for species or individual recognition. In one experiment we reared rock bass (*Ambloplites rupestris*) in social isolation and in social groups. Both the isolated and group-reared fish spent significantly more time close to conspecifics than to heterospecifics. These results suggest that species recognition in rock bass is controlled by a closed genetic program and that social experience is not necessary. A second set of experiments was conducted to determine if year-old bluegill (*Lepomis macrochirus*), pumpkinseed (*L. gibbosus*), and rock bass juveniles could discriminate between familiar and unfamiliar conspecifics. Bluegill spent significantly more time with familiar conspecifics than with unfamiliar conspecifics, while the other two species displayed no such trend. Bluegill spent significantly more time with familiar conspecifics than did either of the other two species. We postulate that these interspecific differences in recognition abilities may be related to differences in habitat and group parameters among the species.

Introduction

Recent interest in recognition abilities has centered on kin recognition (eg. O'Hara and Blaustein 1981; Waldman 1981; Holmes and Sherman 1982; Quinn and Busack 1985) while past interest focused on mate recognition, parent-young recognition, and recognition of rivals in social contests (reviewed in Colgan 1983). An important but often neglected aspect of recognition studies is the ecological context within which the animal operates (Johnston and Gottlieb 1981). In their study on species identification in mallard ducklings (*Anas platyrhynchos*) Johnston and Gottlieb suggested that the natural context of development, the situation within which the animal and the process (imprinting) operate, must be understood before any meaning could be given to laboratory findings. Some recent papers on recognition abilities of fishes have used the ecological context in interpreting the results (Barnett 1982; Myrberg and Riggio 1985; Quinn and Busack 1985). In this study we tested the species and individual recognition abilities of some centrarchid fishes in laboratory experiments and examined the ecological context within which the processes operate.

In the first set of experiments we examined species recognition in three species of centrachid fishes. Studies on species recognition have shown that young fish distinguish species-typical markings and conspecific odours (McCann and Matthews 1974; Barnett 1982; review in Liley 1982). Ernst Mayr (1974), in an interesting paper on behavioural strategies, postulated that species recognition in many animals is controlled by a closed genetic program, one that does not allow for appreciable modification during the process of translation into the phenotype. Some exceptions are certain species of waterfowl and finches. The situation in fishes is not totally clear. Research has been done on species recognition but most have concentrated on adults collected from the wild (reviewed in Liley 1982). One of the few developmental studies, where prior experience of the fish was controlled, was done by McCann and Matthews (1974) who suggested that species identity in zebra fish (*Brachydanio rerio*) is a result of both experiential and innate factors. We chose three sympatric species, the rock bass (*Ambloplites rupestris*), bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish, to examine the contrasting predictions from Mayr's and McCan and Matthew's hypotheses. If social experience is important, then fish reared in social isolation (physically and visually isolated from conspecifics) should respond differently to conspecifics than fish reared with conspecifics. The three species were chosen because much is known of their early life history (Brown 1985; Brown and Colgan 1982, 1984, 1985; Keast 1980; see below).

A second set of experiments examined individual recognition in older centrarchids. Most reports of individual recognition in fish have been concerned with recognition in territorial or hierarchical situations (Nelson 1964; Peeke and Veno 1973; Fricke and Holzberg 1974; Zayan 1975; Gorlick 1976; Colgan et al. 1979; Thresher 1979; Myrberg and Riggio 1985). In these situations it was often difficult to demonstrate clearly that individual recognition was the cue responsible for the response. Role recognition in hierarchies (Gorlick 1976) and location cues in territorial systems (Thresher 1979) are often as important as individual recognition cues in these situations.

In this experiment, we examined the ability of the above three centrarchid species, to differentiate between familiar conspecifics and unfamiliar conspecifics in a non hierarchical or non territorial situation. These three species differ in many aspects of their early life history (Werner et al. 1977; Keast 1978, 1980; Brown and Colgan 1982). For example, bluegill are generally an open water species occurring close to the water surface in large groups, pumpkinseed occur close to the substrate in the vegetation in small groups or individually, while rock bass are found close to the substrate, in the rocks, in small groups or as individuals. In the laboratory, bluegill and pumpkinseed fry form hierarchies within which status does not appear to be size-dependent (Brown and Colgan 1985). Rock bass on the other hand are territorial during their first summer. These differences in habitat use, group size, and social organization provided a good basis for comparison of the ability of individuals of the three species to both recognise conspecifics (species recognition) as well as familiar individuals (individual recognition).

Methods

All experiments were conducted at the Queen's University Biological Station located on Lake Opinicon at Chaffey's Lock, Ontario. The term "fry" indicates fish which have commenced free-swimming and exogenous feeding, and are in the first summer of life. "Juvenile" refers to sexually immature fish older than one year.

Species recognition

In 1980 and 1981, eggs were collected from rock bass, bluegill, and pumpkinseed nests and brought to the laboratory for rearing. During this time we were unable to rear bluegill and pumpkinseed fry in isolation but rock bass fry were found to be relatively easy to rear in isolation from hatching. In 1982 rock bass fry were used in the trials on species recognition. Fish used in the isolation group (IG) were placed individually in 10 L plastic buckets. Twenty buckets with one fry in each were provided with air stones and natural photoperiod. Water was changed twice weekly and two blackchin shiner fry (*Notropis heterodon*) were placed in each bucket once the rock bass were free-swimming. The shiners were "dither fish" (Barlow 1968) and were used to reduce the appearance of fright behaviour or hyperactivity in the isolated fish. The shiners were chosen because they do not resemble, either morphologically or behaviourally, the stimulus fish with which the IG fry were tested. Fry reared in the social group (SG) were collected from nests (different than the IG) and placed in 90 L aquaria. Four aquaria with 25–40 fry in each were supplied with a continuous flow of lake water and a natural photoperiod. Fry were fed cultured wild plankton or live *Artemia* sp. nauplii daily.

Following pilot studies (May–September 1980–1981), all tests were conducted in two glass aquaria, 50 × 27 × 30 cm high, divided into three compartments by glass partitions. The compartments were not water tight. The two end compartments were 10 cm long and the central test area was 30 cm. The test area was divided into two grids (15 cm) by vertical black lines drawn on the glass. In each trial a pair of rock bass was placed in one end compartment and a pair of pumpkinseed sunfish (matched for size) was placed in the other. These stimulus fish were trapped from the lake. Pumpkinseeds were chosen because they are sympatric with rock bass in Lake Opinicon, are readily available, and are easy to maintain in the laboratory.

A single test fish (from one of the two groups) was placed in the test area. Opaque barriers prevented visual contact among fish during the two-hour acclimation period. Following this, the barriers were removed and a five-min observation period began. During this period the position of the fry was recorded each time it switched grids. The timing of the fry in a grid began when its head was in that grid. After the first five-min period the opaque barriers were replaced and the stimulus fish (rock bass and pumpkinseed) placed in the opposite end compartment. After a 10–15 min period a second five-min period was run. Thus, a record of the total time spent in each grid for each period was obtained. At the end of the second period, all fish were measured. An individual fry was tested once only. At the time of testing all fry were at least 26 mm in total length (approximately 2 $^1/_2$ months from hatching), at which size rock bass fry have well developed agonistic behaviour (Brown and Colgan 1985).

Qualitative observations on the behaviour and activity of the stimulus fish were carried out. The activity levels (very active, moderately active, or inactive) and aggressive responses (see Brown and Colgan 1985 for details) of all fry during a trial were noted.

Individual recognition

One-year-old rock bass, pumpkinseed, and bluegill juveniles were captured in the lake and brought into the laboratory for testing. All fish were aged based on total length (Keast 1978). Ten minnow traps were placed in widely separate areas of the lake and checked daily. When more than five similarly-sized conspecific yearlings were found in one trap, they were designated a group. Between five and eight conspecifics from one trap were then transferred to the laboratory and placed together in a 90 L holding aquarium. They were held together from three to seven days before testing. Individuals from a group were tested only once, but could be used as stimulus fish more than once. Holding aquaria were supplied with a continuous flow of lake water, natural photoperiod, and plant cover. Fish were fed daily.

Following preliminary experiments (June–August 1980–1981), two experimental glass aquaria, 90 × 50 × 40 cm high, were divided into three compartments by glass partitions. The two end compartments were 15 cm and the central test area was 60 cm long. The test area was divided into five 12 cm grids by vertical black lines drawn on the glass. In each trial a test fish was placed in the test area, two familiar group members were placed in one end compartment, and two unfamiliar conspecific non group members in the other end compartment. During preliminary experiments it was observed that a single stimulus fish often did not behave normally (would remain motionless, or swim quickly) thus two familiar (group) and two unfamiliar (non group) stimulus fish were used. Non group members were conspecifics caught in other areas of the lake and held in a separate group in the laboratory.

Sizes of all the fish were matched as closely as possible before a trial. Opaque barriers were in place to present visual contact during a two-hour acclimation period, after which a 10-min observation period began. During the observation period a record was made each time the test fish changed grids. A record of the time spent in each grid was thus obtained. At the end of the first observation period the positions of the two pairs of stimulus fish were exchanged and, after a 10–15 min interval, a second period was run. Again the total time the test fish spent in each grid was used in the analysis. Statistical significance was set at 0.05. All fish were measured at the end of the trial and returned to their holding aquaria. Activity levels and aggressive behaviour of the stimulus fish were noted as in previous experiment.

A confounding variable in recognition studies is a binary pattern of recognition, familiar versus unfamiliar (Myrberg and Riggio 1985). Myrberg and Riggio overcame this problem in their study on acoustic recognition in a coral reef fish by presenting a familiar cue (neighbouring male sound) from an unfamiliar location (another direction). It is more difficult to control for this binary pattern of recognition when visual or olfactory modalities are being investigated. It would be extremely difficult to show individual recognition without using a familiar class of stimuli because it seems unlikely that an individual could discriminate among unfamiliar individuals. Exceptions to this would be some forms of kin recognition (phenotype matching) where unfamiliar conspecifics are recognized as relatives (Holmes and Sherman 1982).

In order to demonstrate individual recognition it would be necessary to have an individual discriminate among familiar individuals. This type of study is difficult and could be confounded by factors such as role recognition, immediate prior experience, and location cues. A prerequisite for individual recognition is the ability to discriminate between familiar and unfamiliar stimuli. If this discrimination is free of hierarchical or territorial cues then this would strongly suggest an ability to recognise individuals.

Results

Species recognition

No significant differences were found between the two observation periods of a trial for either the IG rock bass fry (Wilcoxon matched-pairs signed-ranks test; $T=81$, $n=20$) or the SG Fry ($T=62$, $n=20$). When the results for the two periods were pooled, both the IG and SG fry spent significantly more time close to the rock bass than to the pumpkinseed stimulus fish ($Z=2.59$, $n=40$, $P=0.005$; $Z=2.38$, $n=40$, $P=0.007$) respectively. IG rock bass spent a mean of 187.6 s (SE = 12.8) in the grid close to rock bass and a mean of 112.4 s (SE = 13.9) in the grid close to pumpkinseed. SG rock bass values were 180.3 s (SE = 14.9) in the grid close to rock bass and 119.7 s (SE = 15.1) close to pumpkinseed.

The IG fry did not spend more time close to the rock bass than the SG fry ($U_{20,20}=158$). Finally, no significant differences were found in the first choice of the fry from the two groups.

There were no significant differences across treatments in the sizes of pumpkinseed (Kolmogorov-Smirnov two sample test; $K_D=5$, $n1=n2=40$; $K_D=7$, $n1=n2=40$) or rock bass fry used as stimulus fish ($P>0.05$) (Table 1). SG and IG fry were not significantly different in size.

Table 1. Mean sizes (mm total length) and standard error (SE) of the two treatment groups (Isolated and Social) of rock bass (RB) fry and the stimulus fry [rock bass (RB) or pumpkinseed (PS)] in the species recognition experiment. $n=20$ for the treatment groups, $n=40$ for the stimulus fry

	$\bar{X}$ Size	SE
Isolated RB	26.5	0.25
Stimulus RB	26.2	0.28
Stimulus PS	23.5	0.17
Social RB	26.0	1.56
Stimulus RB	26.8	1.82
Stimulus PS	25.1	0.34

Table 2. Mean time (s, $\bar{X}$), standard error (SE) and number of fish tested (n) in the individual recognition experiment. Values are given for the time spent in the closest grid and the two closest grids to group members (GP) and to non group members (N-GP). Refer to text for details

	Closest grid			Closest two grids	
	$\bar{X}$	SE	n	$\bar{X}$	SE
Bluegill					
GP	237.5 (s)	17.8	30	303.8 (s)	18.4
N-GP	150.3 (s)	12.5	30	230.4 (s)	16.6
Pumpkinseed					
GP	185.4 (s)	10.4	20	254.3 (s)	21.4
N-GP	208.6 (s)	22.3	20	263.2 (s)	23.2
Rockbass					
GP	208.6 (s)	13.4	23	256.3 (s)	23.6
N-GP	244.7 (s)	18.2	23	306.1 (s)	24.0

Table 3. Mean sizes (mm total length), standard errors (SE), and number of fish tested (n) for the test fish (Test), group members (GP), and non group members (N-GP) in the individual recognition experiment

	Bluegill			Pumpkinseed			Rock bass		
	Test	GP	N-GP	Test	GP	N-GP	Test	GP	N-GP
$\bar{X}$ Size	53.6	52.3	51.6	54.9	53.2	54.5	58.7	57.9	56.2
SE	1.2	1.3	1.2	1.0	1.5	0.8	1.4	0.8	0.9
n	30	60	60	20	40	40	23	46	46

Little aggression was observed in any of the trials. In general, stimulus fish were moderately active and no difference in behaviour by the two species of stimulus fish towards the test fish were observed.

Individual recognition

Juvenile bluegill sunfish spent significantly more time in the grid closest to group members than in the grid closest to non group members (Wilcoxon; $Z=3.03$, $n=60$, $P=0.001$) (Table 2). No significant differences were found in the time spent in the grid closest to group members compared to the time spent in the grid closest to non group members for pumpkinseed ($T=0.76$, $n=40$, $P=0.230$) or rock bass juveniles ($Z=1.21$, $n=46$, $P=0.113$) (Table 2). These same results were found when the time spent in the *two* grids closest to group members was calculated. Bluegill spent significantly more time close to group members ($T=2.04$, $n=60$, $P=0.002$) whereas pumpkinseed ($T=0.76$, $n=40$, $P=0.224$) and rock bass juveniles ($Z=-1.4$, $n=46$, $P=0.081$) did not (Table 2). Bluegill test fish spent more time close to group members than did either pumpkinseed (Mann-Whitney; $Z_{20,30}=2.34$, $P=0.009$) or rock bass ($Z_{23,30}=2.60$, $P=0.005$) test fish.

Size has often been reported to be an important cue with regards to social processes in fish (Henderson and Chiszar 1977). The mean sizes for the test and stimulus fish in this experiment are given in Table 3. To determine if size of the test and stimulus fish influenced the choice, the data were examined using size of fish as a variable. Bluegill did not spend more time close to group members when they were larger or smaller than both group members, larger or smaller than both non group members, larger than one group member, or larger than one non group member (Wilcoxin, $P>0.05$). Pumpkinseed and rock bass juveniles displayed the same lack of trend except that rock bass spent more time close to group members when they were larger than one non group member ($T=6.00$, $n=10$, $P<0.05$).

As well as the absolute size of the fish involved, the relative sizes of the fish in a test situation may influence the results. We compared the time spent close to group members to the ratio of the total length of group fish over the total length of non group fish for each trial. No association was found between this ratio and time spent close to group members for bluegill (Spearman rank coefficient; $T=0.714$, $df=28$), pumpkinseed ($T=0.774$, $df=18$), or rock bass juveniles ($T=1.20$, $df=21$). Thus confounding effects due to size were not apparent for any of the species tested.

Aggressive interactions between the test and stimulus fish were observed in less than 7% (10/146) of the trials. Rock bass test fish were aggressive in 15% (7/46) of their trials while stimulus bluegills were aggressive towards test fish in 0.5% (3/60) of their trials. The aggression of test rock bass was divided towards non group members on four occasions. All stimulus fish were moderately active and no observable differences in the behaviour of the various stimulus fish towards test fish were noted.

Discussion

Species recognition

The results indicate that social experience is not necessary for species recognition in young-of-year rock bass. Rock bass socially isolated from early life spent more time in close proximity to rock bass stimulus fish than to pumpkinseed stimulus fish. A second group of rock bass reared in social groups displayed the same trend.

Investigations of social recognition must avoid confounding by such extraneous influences as novelty. In this regard both the rock bass and pumpkinseed stimuli were novel to the isolated rock bass and so this factor is not a concern. Vision is the most likely modality used by the rock bass. Centrarchids (including the species studied here) have been shown to be visual feeders (Keast 1978; Mittelbach 1981). Visual cues have also been demonstrated to be important in their reproductive activities (Colgan et al. 1979). Even though olfaction may be important in certain situations (such as high turbidity) there is no evidence to date which indicates that centrarchids in Lake Opinicon use olfaction in their daily activities. Thus our experimental protocol, though simple, does provide evidence for species recognition.

The positive response of the two laboratory groups indicate that an experiential factor, as suggested by McCann and Matthews (1974), is not necessary for species recognition in rock bass.

The reason for the difference between the present study and that of McCann and Matthews may be related to differences in the early life history of the species studied. McCann and Matthews examined the problem in a schooling species, the zebra fish, and it may not be necessary for species recognition to be controlled by a closed genetic program. The reason is that under normal circumstances this type of individual will be in a school of conspecifics in open water. In this situation individuals could "learn" their species identity by association with conspecifics. In a later study McCann and Carlson (1982) demonstrated that zebra fish, cross-reared with pearl danios (*Brachydanio albolineatus*), showed less intense species identity than did controls. Thus in schooling species the *tendency* to school may be controlled by a closed genetic program and species recognition controlled by an open genetic program. Some support for this comes from the work of Williams and Shaw (1971) on schooling in *Menidia menidia.* They found that schooling tendency persisted in individuals reared in social isolation but these individuals differed from group-reared ones in over-all schooling pattern and in interactions between fish within a school. Young rock bass have never been observed to display any group behaviours (approach, schooling) during their early free-swimming life (Brown and Colgan 1984, 1985; Brown 1985). As well, young rock bass vacate the nest individually or in small groups and are found hiding among the gravel on the substrate (Brown 1985). The possibility of individuals becoming separated is relatively high compared to individuals which school in open water. Thus, for rock bass and species which do not school and have a high probability of becoming separated from conspecifies during their early life history, species recognition may be controlled by a closed genetic program.

There are analogous situations in birds. In many species of waterfowl the process of imprinting apparently operates under a closed genetic program (innate) while species recognition is learned, i.e. open, (Johnston and Gottlieb 1981). However, in some parasitic finches species recognition operates under a closed genetic program (Mayr 1974).

Individual recognition

The results on individual recognition indicate that juvenile bluegill preferred to be in closer proximity to familiar group members than to unfamiliar non group members. Pumpkinseed and rock bass juveniles displayed no such trend. This finding is consistent with an earlier report by Butler and Johnson (1972) that, in an operant conditioning situation, bluegill showed an indication of discriminating individual conspecifics. The results of the present study were not based on any apparent size factor among the fish tested. It appears that bluegill sunfish can recognize individuals from a group in which they have been resident for a period of time. As argued previously, the observation that fish can discriminate between a sub-group of familiar and unfamiliar conspecifics outside of a strict hierarchical or territorial situation provides compelling evidence for individual recognition. Given that the protocol was identical for all three species, we suggest that our experiment has provided evidence that juvenile bluegill can recognize individuals. There are two proposed social contexts which can favour individual recognition, stable dominance hierarchies and kinship-based recognition systems.

Barnard and Burke (1979) have argued that individual recognition can be selected in certain types of hierarchies, such as assessment hierarchies, which are based on an individual's ability to assess cues received from an opponent. They conclude that individual recognition is not a prerequisite for dominance hierarchies but that dominance hierarchies may be a driving force for the evolution of individual recognition. However, in order for this to occur, the groups must be relatively stable over time. If there is a high turnover of individuals in a group, then it would be extremely difficult for an individual to be able to recognize individuals due to the high number of fish encountered.

There are no data on the stability of bluegill aggregations over time but certain aspects of their life history suggest that group stability may exist. In Lake Opinicon and elsewhere, bluegills tend to be more associated with open water and are observed in larger groups than the other two species (Werner et al. 1977; Keast 1978; Brown and Colgan 1982). Even though bluegills are observed in weed beds it is typically in the open areas of these beds (Brown and Colgan 1982). If in an open water environment, groups are more likely to stay together, then individual bluegill are more likely to encounter the same conspecifics over time. Further speculation is not warranted. However, as Breed and Bekoff (1981) point out, under these conditions kin recognition, involving individual recognition, may also evolve.

Bluegill would also be the most likely of the three species to remain with kin over time. The reproductive habits of the species are similar (Gross 1982). The offshore group activities of the fry are unknown but bluegill and pumpkinseed fry probably remain together due to schooling or aggregating behaviour (J.A. Brown, personal observation). If bluegill are more likely to remain in the same group than are pumpkinseed or rock bass then individual recognition in bluegill could function as a kinship-based recognition system.

Quinn and Busack (1985) have recently found that juvenile coho salmon (*Oncorhynchus kisutch*) can recognize siblings. They suggest that individual salmon can increase their inclusive fitness by joining schools of kin. A fish joining a school increases the fitness of each member in the group and if the other members of the school are kin, the increase in inclusive fitness is greater than if they are non kin. Individual recognition in bluegill may increase an individual's inclusive fitness in a school of kin. Ferguson and Noakes (1981) have provided some evidence that gene frequencies among groups of shiners (*Notropis cornutus*) are more heterogeneous than gene frequencies within groups.

If either of these scenarios is correct, then the following predictions result. One is that group stability is greatest for bluegill. This would provide support for both Barnard and Burke's (1974) and Breed and Bekoff's (1981) proposals. However, a second prediction is that genetic relatedness will be higher in groups of bluegill than in pumpkinseed or rock bass. A positive finding for this prediction would support a kinship-based recognition system, while a negative finding would provide support for the hierarchy function of individual recognition. In general, fish species which show long-term group stability are likely to display individual recognition abilities. In species where group stability is low, individual recognition ability is less likely except in certain situations (i.e. territorial).

Acknowledgements. We appreciate the excellent facilities provided by the Queen's University Biological Station, and thank its director, R.J. Robertson, and manager, F. Phelan. Dr. J.M. Green kindly provided space for the senior author, which is greatly appreciated. We thank L. Fahrig and J. Templeton for their assistance in maintaining the fish. Dr. P.H. Johansen, V. Gotceitas, M.J. Morgan, and J.J. Templeton made helpful comments on an earlier draft. We especially thank Drs. M. Gross and J. Rice for insightful suggestions. Financial support was provided by an N.S.E.R.C. Operating Grant to P.W.C.

References

Barlow GW (1968) Dither – A way to reduce undesirable fright behavior in ethological studies. Z Tierpsychol 25:315–318

Barnard CJ, Burke T (1979) Dominance hierarchies and the evolution of "individual recognition". J Theor Biol 81:65–73

Barnett C (1982) The chemosensory responses of young cichlid fish to parents and predators. Anim Behav 30:35–42

Breed MD, Bekoff M (1981) Individual recognition and social relationships. J Theor Biol 88:589–593

Brown JA (1985) The adaptive significance of behavioural ontogeny in some centrarchid fishes. Environ Biol Fish 13:25–34

Brown JA, Colgan PW (1982) The inshore vertical distribution of young-of-year *Lepomis* in Lake Opinicon, Ontario. Copeia 1982:958–960

Brown JA, Colgan PW (1984) The ontogeny of feeding behaviour in four species of centrarchid fish. Behav Proc 9:395–411

Brown JA, Colgan PW (1985) The ontogeny of social behaviour in four species of centrarchid fish. Behaviour 92:254–276

Butler M, Johnson DA (1972) A test of individual recognition in bluegill sunfish using operant procedures. Va J Sci 23:149

Colgan PW (1983) Comparative social recognition. Wiley & Sons, New York

Colgan PW, Nowell WA, Gross MR, Grant JWA (1979) Aggressive habituation and rim circling in the social organization of bluegill sunfish (*Lepomis macrochirus*). Environ Biol Fish 4:19–36

Ferguson MM, Noakes DLG (1981) Social grouping and genetic variation in common shiners, *Notropis cornutus* (Pisces Cyprinidae). Environ Biol Fish 6:357–360

Fricke HW, Holzberg S (1974) Social units and hermaphroditism in a pomacentrid fish. Naturwissenschaften 61:367–368

Gorlick DL (1976) Dominance hierachies and factors influencing dominance in the guppy, *Poecilia reticulata* (Peters). Anim Behav 24:336–346

Gross MR (1982) Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. Z Tierpsychol 60:1–26

Henderson DL, Chiszar DA (1977) Analysis of aggressive behaviour in the bluegill sunfish *Lepomis macrochirus* Rafinesque: Effects of sex and size. Anim Behav 25:122–130

Holmes WG, Sherman PW (1982) The ontogeny of kin recognition in two species of ground squirrels. Am Zool 22:491–517

Johnston TD, Gottlieb G (1981) Development of visual species identification in ducklings: What is the role of imprinting? Anim Behav 29:1082–1099

Keast A (1978) Feeding interrelations between groups of pumpkinseed (*Lepomis gibbosus*) and comparisons with bluegill (*L. macrochirus*). J Fish Res Board Can 35:12–27

Keast A (1980) Food and feeding relationships of young fish in the first weeks after the beginning of exogenous feeding in Lake Opinicon, Ontario. Environ Biol Fish 5:304–314

Liley NR (1982) Chemical communication in fish. Can J Fish Aquat Sci 39:22–35

Mayr E (1974) Behavioral programs and evolutionary strategies. Am Sci 62:650–659

McCann CI, Matthews JL (1974) The effects of lifelong isolation on species identification in zebra fish (*Brachydanio rerio*). Dev Psychobiol 7:159–163

McCann CI, Carlson CC (1982) Effect of cross-rearing on species identification in zebra fish and pearl danios. Dev Psychobiol 15:71–74

Mittelbach GG (1981) Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. Ecology 62:1370–1386

Myrberg AA Jr, Riggio RJ (1985) Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*). Anim Behav 33:411–416

Nelson K (1964) Behavior and morphology in the glandulocaudine fishes (Ostariophysi, Characidae). Univ Calif Publ Zool 75:59–152

O'Hara RK, Blaustein AR (1981) An investigation of sibling recognition in *Rana cascadae* tadpoles. Anim Behav 29:1121–1126

Peeke HVS, Veno A (1973) Stimulus specificity of habituated agression in the stickleback (*Gasterosteus aculeatus*). Z Tierpsychol 40:53–58

Quinn TP, Busack CA (1985) Chemosensory recognition of siblings in juvenile coho salmon (*Oncorhynchus kisutch*). Anim Behav 33:51–56

Thresher RE (1979) The role of individual recognition in the territorial behaviour of the threespot damselfish, *Eupomacentris planifrons*. Mar Behav Physiol 6:85–93

Waldman B (1981) Sibling recognition in toad tadpoles: The role of experience. Z Tierpsychol 56:341–358

Werner EE, Hall DJ, Caughlin DR, Wagner DJ, Wilsmann LA, Funk FC (1977) Habitat partitioning in a freshwater fish community. J Fish Res Board Can 34:360–370

Williams MM, Shaw E (1971) Modifiability of schooling behavior in fishes: The role of early experience. Am Mus Novit 2448:1–19

Zayan RC (1975) Défense du territoire et reconnaissance individuelle chez *Xiphophorus* (Pisces, Poeciliidae). Behaviour 52:266–312