Facultative schooling behavior in the spottail shiner (*Notropis hudsonius*): possible costs and benefits

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Synopsis

If an individual is less susceptible to predation in a group it should be able to reduce its vigilance for predators and perhaps also its tendency to flee from predators, thereby gaining time and energy for feeding and other activities. These predictions were examined in the field (Veronica Lake, northwestern Ontario) using a facultative schooling species, the spottail shiner (*Notropis hudsonius*). Schools of various sizes 'attacked' with a fish predator model had a significantly lower reaction distance to the predator than solitary shiners. Solitary shiners must therefore invest more time and energy in defense but may gain a feeding advantage because their visual field does not overlap with conspecific competitors.

Introduction

Theoretical models in sociobiology have emphasized the role of food resources and predator defense as major ultimate determinants of sociality (Alexander 1974, Brown 1975, Wilson 1975, Bertram 1978, Rubenstein 1978). If an individual is less susceptible to predation in a group it should be able to reduce its vigilance for predators and perhaps also its tendency to flee from predators thereby gaining time and energy for feeding and other essential activities. Several studies of gregariousness in birds (Lazarus 1978, 1979, Lazarus & Inglis 1978, Powell 1974, Siegfried & Underhill 1975, Smith 1977) and mammals (Hamilton et al. 1978, Berger 1978, Hoogland 1979) have examined these predictions but it has not been established if fish schools conform to this pattern. In this paper I present field data showing that spottail shiners (*Notropis hudsonius*) in schools are less responsive than solitary shiners to a potential predator.

Field observations

I studied the behavior of juvenile shiners (< 2 mo old) in a shallow sandy bay of Veronica Lake, a 120 ha oligotrophic lake 50 km southeast of Kenora, Ontario, Canada. The shiners have a relatively simple time-energy budget at this early life history interval: they must feed on zooplankton, grow quickly before the onset of the five-month period of ice cover, and escape the attacks of juvenile and adult yellow perch (*Perca flavescens*), the only major piscivores present during the summer growth period.

Most of the juvenile shiners occur within 2 m of shore in water less than 25 cm deep. The shiners share this habitat with the juvenile perch who spend considerable time and effort chasing the shiners,

thus forcing the shiners to interrupt their feeding, alter their swimming path, and often make vigorous escape movements. The size relationship between juvenile shiners and juvenile perch is illustrated by samples taken with a fine mesh seine in mid-July 1978 (Fig. 1). Most of the predator-prey interactions occur between the larger members of the juvenile perch stock and the smaller members of the shiner stock. Older perch (1+ and 2+ year class) appear infrequently in the shallow water as they dart in from deeper water to attack both the shiners and juvenile perch. The antipredator behavior of the shiners resembles the description given by Nursall (1973) for adult spottail shiners in Alberta, Canada.

The shiners may occur singly or in schools, i.e. they are facultative schoolers (Shaw 1978). Schools consist of two or more fish of similar size swimming together in a coordinated (usually polarized) fashion, 1 to 6 body lengths apart. Single fish are not affiliated with a school and are usually farther than 50 cm from the nearest shiner. They may, however, eventually form or join a school. Few schools maintain their integrity for more than a minute

(Evered & Seghers, in preparation) supporting Radakov's (1973) generalization that the composition of schools of planktivorous fish is highly unstable.

Size of shiner schools

To determine the number of fish in a school I walked slowly along a 145 m beach and recorded the frequency of single fish and fish in various school sizes. To obtain accurate estimates for schools larger than five fish, repeated counts were made using a mechanical tally counter. Observations were made in the late afternoon (1620 - 1930 h); water temperature varied from 19.5° C to 22.5° C and illuminance (measured over the water surface with a light meter) ranged from 11,000 to 60,000 1 ×.

School size varied from 2 to 49 fish but in 39.8% (195/490) of the observations or 12.3% (195/1587) of the total number of fish counted, the shiners were not schooled (Fig. 2). Almost 50% of the shiners were distributed as solitary fish and schools of less than five fish.
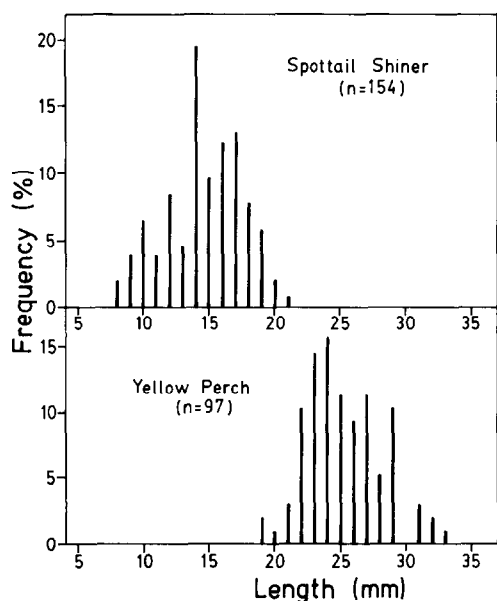

Fig. 1. Length (total) frequency histogram of juvenile spottail shiners (prey) and juvenile yellow perch (predators) co-occurring in the littoral zone of Veronica Lake, northwestern Ontario. Samples were taken in mid-July, 1978.
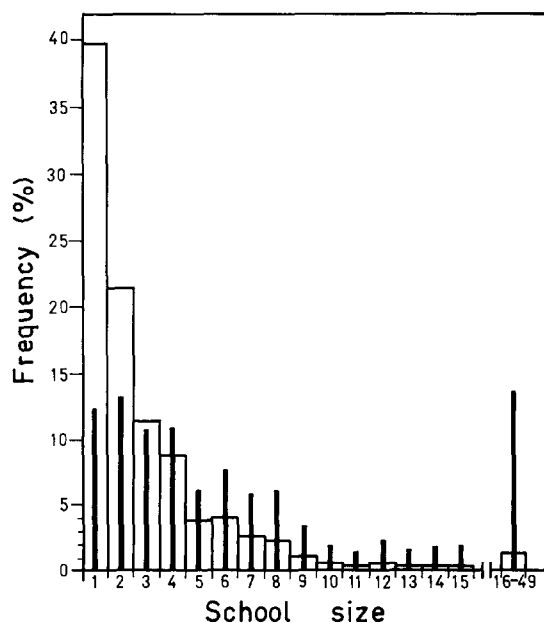

Fig. 2. Distribution of school sizes and individual membership in schools of juvenile spottail shiners, Veronica Lake, mid-July, 1978. Histograms indicate frequency of schools of a particular size (490 observations), whereas black bars indicate the percent of 1587 individuals that occurred in schools of a particular size.

Response to simulated predator attack

I measured the response of the shiners to a potential predator by 'attacking' a single fish or an entire school with a plastic 10 cm fishing lure (hooks removed) resembling a pike (overall green in color and countershaded) mounted on the end of a 1.8 m glass rod. The attack began 1 m from the fish at a constant approach velocity of 20 cm s^{-1} (controlled manually). I recorded to the nearest 10 cm the distance at which the individual fish or school fled from the predator model ('reaction distance'). Because it was not possible to perceive individual differences in reaction distance among school members, a single distance was recorded for the entire school. Control tests were conducted in an identical manner without a lure on the glass rod. This resulted in reaction distances of 0 – 5 cm indicating that the fish were reacting to the predator model and not my movements.

Results of 176 tests revealed that shiners in schools had a significantly shorter reaction distance than solitary shiners (p < 0.001, t-test); however, there was no difference among the various school sizes (Fig. 3).

Discussion

The relative probability that an individual will be captured, once detected, should be approximately 1/N where N is the school size. It is therefore surprising that the presence of only a single companion had the same effect on the escape threshold as many companions. Theoretically individuals in schools larger than two could have 'afforded' to relax their reaction distances more. The escape threshold of the juvenile shiner therefore seems to have only two basic settings, high for individuals and low for schools.

Although the reaction distance for escape did not change as a function of school size, it is possible that the predator was detected sooner or at a greater distance in larger schools (cf. Nikolsky 1955, cited in Radakov 1973) as has been demonstrated for other vertebrate social groups (Powell 1974, Siegfried & Underhill 1975, Carl 1971, Hoogland & Sherman 1976, Kenward 1978, Hoogland 1979). This phenomenon has been termed the 'early
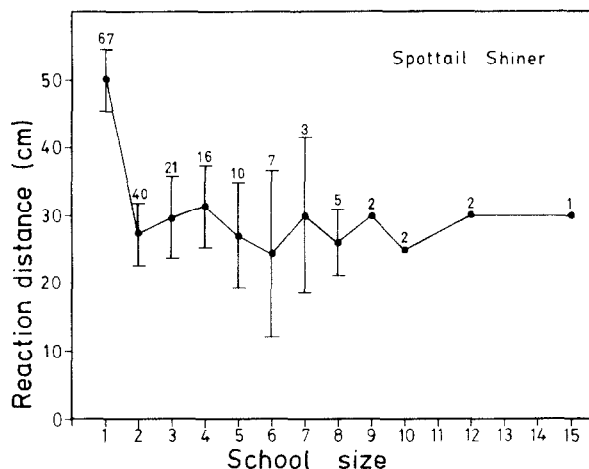

Fig. 3. The relationship between school size of spottail shiners and reaction distance to a predator model. Tests were conducted on calm, sunny days (approximately 0900 - 1800 h) in mid-July, 1978. The number of replicate tests is shown above each mean; vertical lines are $\pm$ 2 SE.

warning function' of social groups (Lazarus 1979). Under the present field conditions it was not possible to discern subtle changes in behavior such as eye movements or orienting reactions. Laboratory experiments are in progress to examine this (Abrahams & Seghers, in preparation).

Why do solitary fish occur so frequently? This is puzzling because recent field work in Veronica Lake (Seghers, in preparation) has revealed that the perch attack solitary shiners preferentially. Also, there is a growing body of evidence confirming that single fish are indeed more vulnerable to predators than schooled fish (Radakov 1973, Neill & Cullen 1974, Major 1978, McKaye et al. 1979). Single fish have a large 'domain of danger' (Hamilton 1971) and when viewed against the visual background of a school they might appear spatially odd to a predator (Milinski 1977) and hence be at a greater risk. Moreover, they cannot benefit from the 'confusion effect' of schools (Hobson 1978, Moss 1979).

Although the shiners presumably could reduce the time and energy allocated to antipredator behavior by associating permanently in schools, there is a potential benefit to solitary fish that may partially offset the increased cost of defense. Eggers (1976) has shown mathematically that schooling is disadvantageous for planktivores because the visual field of each individual overlaps partially with that

of others in the school. This may result in competition for zooplankton. If this hypothesis is correct, shiners may alternate between a schooled and solitary strategy as a function of hunger. This is supported by the general observation that feeding fish form less cohesive schools (Keenleyside 1955, Hunter 1966). Perhaps the high frequency of very small schools observed in this study reflects the best compromise between avoiding intraspecific competition for food and predation by perch.

Acknowledgements

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