

Foraging and Prey Search Behaviour of Golden Shiner (*Notemigonus crysoleucas*) Larvae

Howard I. Browman¹ and W. John O'Brien

Department of Systematics and Ecology, The University of Kansas, Lawrence, KS 66045-2106, USA

Browman, H. I., and W. J. O'Brien. 1992. Foraging and prey search behaviour of golden shiner (*Notemigonus crysoleucas*) larvae. *Can. J. Fish. Aquat. Sci.* 49: 813–819.

The juveniles of several species of freshwater fish search for zooplankton prey using a strategy intermediate between cruise and ambush: "saltatory search" (SS) or "pause-travel" search. Unlike ambush or cruise search, saltatory search involves scanning for prey throughout the search space and only during the brief stationary periods that punctuate repositioning movements. If no prey are located, these fish swim a short distance, stop, and scan again. In this paper, we describe the ontogeny of prey search in a cyprinid, the golden shiner (*Notemigonus crysoleucas*), a species whose search pattern has not been examined. Swimming and pursuit speeds and prey location distances increased with fish size. Golden shiner larvae searched for prey throughout the search space and only during the pauses that punctuated swimming movements. Only 1–10% of all of the stationary pauses that punctuated swimming movements were followed by attacks on prey. We conclude that golden shiner larvae employ a saltatory-search strategy similar to that described in other zooplanktivorous fish and their larvae.

Les juvéniles de plusieurs espèces de poissons d'eau douce chassent leurs proies zooplanctoniques en utilisant une stratégie intermédiaire entre le déplacement continu et l'affût : la stratégie «saltatoire» (SS) ou «d'arrêt et déplacement». À la différence de la recherche de proies par déplacement continu ou à l'affût, la stratégie saltatoire consiste à localiser les proies dans tout l'espace de recherche seulement durant les courtes périodes stationnaires entre les déplacements. Si aucune proie n'est localisée, ces poissons nagent sur une courte distance, s'arrête, puis tente à nouveau de localiser des proies. Dans le présent article, nous décrivons l'ontogénie du comportement de recherche de proies d'un cyprinidé, la chatte de l'est (*Notemigonus crysoleucas*), comportement qui n'a jamais été étudié chez cette espèce. La vitesse à laquelle elle nage et poursuit ses proies de même que la distance à laquelle elle peut localiser ses proies s'accroissent en raison directe de sa taille. Les larves de la chatte de l'est recherchent leurs proies dans tout l'espace de recherche et seulement durant les pauses entre leurs déplacements. Seulement 1 à 10 % des pauses stationnaires ont été suivies d'une tentative de capture de proie. Les larves de la chatte de l'est ont recours à une stratégie saltatoire semblable à celle déjà observée chez d'autres poissons zooplanctivores et leurs larves.

Received May 6, 1991

Accepted October 24, 1991

(JB026)

Reçu le 6 mai 1991

Accepté le 24 octobre 1991

Zooplanktivorous fish are often important predators in aquatic ecosystems and are known to have pronounced effects on the population dynamics of their prey (Lazzaro 1987). To elucidate their role as predators, the feeding modes, selectivities, and search patterns of juvenile and adult planktivores have all been examined in some detail (O'Brien 1979; O'Brien et al. 1986, 1989; Lazzaro 1987; Wetterer 1989; O'Brien et al. 1990).

Virtually all fish are planktivorous at some time during ontogeny, and because of the importance of early life history stage dynamics to fisheries biologists (e.g. Sinclair 1988), the foraging behaviour of fish larvae has been studied extensively (Hunter 1980; Brown and Colgan 1984, 1985; Blaxter 1986; Noakes and Godin 1988). Until recently, however, the ontogeny of prey search strategies in fish larvae, and how these relate to those of juveniles and adults, has received only limited attention (Browman and O'Brien 1992).

Animals, such as zooplanktivorous fish, that forage for discrete, isolated resources are generally characterized as either "ambush" (sit-and-wait) or "cruise" (active) searchers

(McLaughlin 1989; Tye 1989; Bell 1990; O'Brien et al. 1990). Ambush foragers have been characterized as stationary searchers, scanning for prey at the periphery of their strike range. They typically wait for prey to cross the outer boundary of the search space before attacking. Cruise foragers have been characterized as moving more or less continuously, scanning for prey near the outer boundary of their search space. An intermediate search strategy, termed "saltatory search" (SS) by O'Brien et al. (1989, 1990) and "pause-travel" search by Tye (1989), has recently been described in the juveniles of several species of zooplanktivorous fish and in several other taxonomic groups (e.g. Janssen 1982; Ehlinger and Wilson 1988; Ehlinger 1989a; Tye 1989; Ehlinger 1990; reviewed by Bell 1990; O'Brien et al. 1990). Saltatory-searching animals scan for prey throughout the search space, but only during the brief stationary periods that punctuate swimming movements. If prey are not located, the animal moves a short distance, stops, and scans again (O'Brien et al. 1986, 1989, 1990; Evans and O'Brien 1988; Tye 1989).

In a previous study, we examined the ontogeny of prey search in a centrarchid, the white crappie (*Pomoxis annularis*), and found that the larvae of this species employ a search strategy similar to that observed in juveniles (Browman and O'Brien 1992). In that study, we discussed how characterizations of a

¹Author to whom correspondence should be addressed. Present address: Department of Biology, University of Victoria, P.O. Box 1700, Victoria, B.C. V8W 2Y2, Canada.

fish's search pattern could affect the calculation and interpretation of such commonly estimated parameters as prey encounter and feeding rate. In this paper, we examine the generality of the saltatory-search pattern and report the results of experiments in which the ontogeny of foraging and prey search behaviour in the golden shiner (*Notemigonus crysoleucas*) was examined.

Study Species

Golden shiner are widely distributed in North America, commonly inhabiting weedy lakes, ponds, and streams (Scott and Crossman 1973). The species is often one of the most abundant of the ichthyofauna and is a significant consumer of zooplankton biomass (Hall and Ehlinger 1989) as well as an important forage fish in the diet of several gamefish species (Scott and Crossman 1973; Keast 1985; Johannes et al. 1989). Adults (50–70 mm total length (TL)) are usually found in midwater or near the surface in small shoals (Hall et al. 1979), while larvae in mixed-cohort shoals are found in the nearshore littoral zone (Hatch 1988). Eleutheroembryos are approximately 3 mm in length, and fish of 5.0–14.0 mm TL are considered larvae. Transition to the juvenile period occurs at approximately 18 mm TL. The species' development is summarized in Auer (1982, p. 223–228). To our knowledge, no detailed observations on the foraging behaviour of golden shiner larvae have been published.

Materials and Methods

General Procedures

Fertilized golden shiner eggs, deposited on artificial brush nests, were obtained in July 1988 from the Kaw Valley Fish Farm in Douglas County, Kansas, USA. The nests were incubated in aquaria at 26°C on a 14 h light : 10 h dark cycle. Eleutheroembryos were 3.9 ± 0.23 mm TL ($n = 6$) and prey items were first observed in the gut of fish 4.77 ± 0.45 mm in length ($n = 6$) on day 3 post-hatch (DPH).

Larvae were fed on fresh zooplankton, collected from local reservoirs, until they reached a size of 15 mm. Larvae > 15 mm were fed a mixture of zooplankton and *Artemia* nauplii (Argent Laboratories' "Argentemia Silver"). Total prey abundance was $500 \cdot L^{-1}$.

Observations began 4 d after food was first observed in the gut, after the yolk sac had been completely absorbed. The mean total lengths (\pm SD, $n = 5$) of fish observed in the experiments were 6.22 ± 0.24 , 8.44 ± 0.22 , and 21.4 ± 0.9 mm. According to the criteria summarized in Auer (1982, p. 223–228), the fish in the 21.4-mm size class were recently transformed juveniles. When larvae reached 8 mm TL, their numbers had been greatly reduced by mortality. As a result, surviving fish were used in several experiments as they grew.

In all experiments, five fish were placed in a $30 \times 30 \times 30$ cm all-glass observation tank at least 12 h prior to an experiment. The tank was filled with 12 L of water and was devoid of prey items. Its sides were covered with black plastic. Light intensity (diffused sunlight) at the water surface was 100 lx (± 10) and water temperature was 26°C.

At the beginning of an experiment, food items (zooplankton that passed through a 64- μ m mesh) were introduced to the observation aquarium at an abundance of $100 \text{ prey} \cdot L^{-1}$. No clumping of prey was apparent. Prey consisted of copepod nauplii or early copepodites and small cladocerans upon which golden shiner larvae feed in the wild (Keast 1980; Hatch 1988).

The abundance of prey items introduced in the experiments was determined by calculating the mean number of items in three 1-mL subsamples of the source populations and introducing the volume required to yield $100 \text{ items} \cdot L^{-1}$ in the 12-L observation tank. In each experiment, foraging behaviour was videotaped until the five fish had attempted 10–15 attacks on prey. All experiments were conducted between 11:00 and 13:00 and lasted 30 min.

Observations and Analysis of Foraging and Search Behaviour

Silhouette (shadow) video photography was used to record the foraging and prey search behaviour of golden shiner larvae (Arnold and Nutall-Smith 1974). Shadow images were focused on the lens (Nikon 35 mm f/2.0) of Panasonic WV-140 black and white (b&w) videocameras, recorded with Panasonic NV-8420 and General Electric 1CVD5025X videotape recorders, and monitored on b&w television screens.

A small, underrun microscope lamp (12 V, 100 W, filament area 4×2 mm) was used as a point source of light and placed at the first focus of an optical-quality biconvex collimating lens (18 cm in diameter, 333-mm focal length, Edmund Scientific). The lens was oriented for imaging in the vertical plane (from above). To estimate the extent of vertical movement during foraging, a second lens, oriented for synchronous imaging in the horizontal plane (from the side), was used in some experiments. From the point sources of light, these lenses "projected" a collimated beam through the observation tank. The use of a collimated beam prevented perspective distortion; clear, sharp shadows of any organism (even transparent ones) in the beam's path were produced and recorded by the videocameras. The system's resolution was approximately 0.2 mm.

The videotapes were analyzed frame by frame on a video-monitor using a Panasonic AG-1950 videotape machine. All time intervals were measured in increments of 0.033 s. For each experiment, a videotaped ruler established conversions from monitor units to millimetres. Sequences in which movement in the vertical plane exceeded 5° from horizontal were not analyzed (approximately 5% of all sequences).

Search behaviour was analyzed by assigning the activities of the fish to one of the components of their predation cycle: pause, move (swim), or pursuit (Fig. 1a). The fish's swimming movements are abbreviated by pauses, during which the fish is stationary. Pauses can be followed by moves or by pursuits. A move is operationally defined as a swimming movement that is not followed by an attack on prey. A pursuit is a swimming movement that precedes an attack on prey. Pauses prior to moves are termed unsuccessful search times (USST). Pauses prior to pursuits are termed successful search times (SST). The distance from the point at which the fish first reacted to a prey item and the position of the prey itself is the pursuit distance. In this analysis, pursuit distance is interpreted as equivalent to prey location distance.

Move and pursuit distances and angles were marked on the monitor with a grease pencil and measured (Fig. 1b). The longitudinal body axis of the fish was defined as the central axis of the forward-directed visual field (i.e. 0° from forward-directed). Thus, pursuit angle is defined as that angle between the central axis of the fish prior to pursuit and the line connecting the fish's rostrum to the position of the prey (determined as the point at which the fish attacked the prey item, or directly when the prey item could be seen on the screen) (Fig. 1b). Move turn angles were measured as the angle between the fish's body axis at one position and the position of its rostrum at the next (Fig. 1b). The durations of these events

a) Search cycle of golden shiner larvae

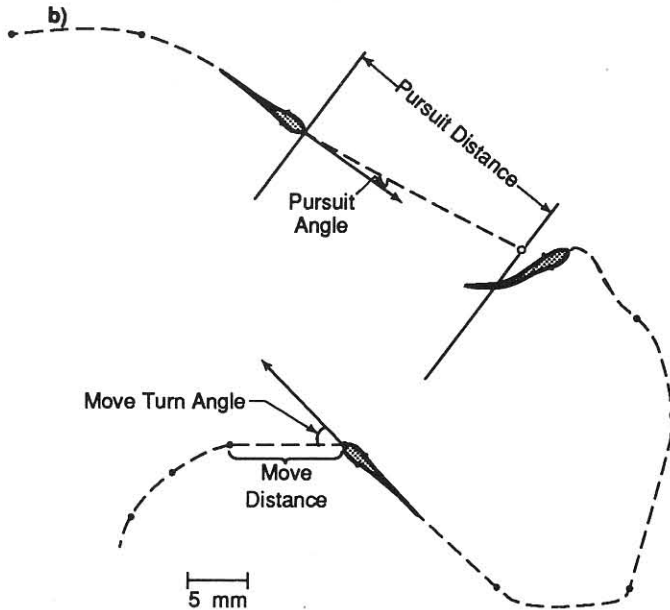
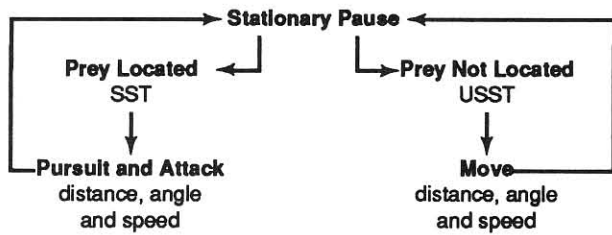


FIG. 1. (a) Flow chart of the predation cycle for golden shiner larvae. (b) A typical search path and attack sequence for golden shiner larvae, sketched directly off of the television screen, illustrating the measurements drawn from it. The solid dots along the broken line represent stationary pauses. The open dot represents a prey item.

and of stationary pauses between them were measured. Move and pursuit speeds were calculated from these measurements.

A multivariate analysis of variance, with a repeated measures design (Statistical package for the social sciences, routine MANOVA), was used to test for the overall effect of fish size on all of the components of the predation cycle. The univariate *F*-tests calculated from the MANOVA were used to evaluate whether fish size had an effect on any isolated component of the predation cycle.

Results

Swimming in golden shiner larvae was punctuated by frequent stops (every 0.17–1.67 s) and reorienting turns (Fig. 1b). Even the smallest individuals observed were relatively strong swimmers, moving through the water without the prolonged periods of rest exhibited by some other fish larvae (e.g. Rosenthal 1969; Hunter 1972; Drost and van den Boogaart 1986; Drost 1987). In any given experiment, approximately 1–10% of stationary pauses were followed by attacks on prey. The entire predation sequence, from prey location through attack, took an average of 1.2 s and did not vary significantly with fish size.

Fish size had a significant overall effect on the components of the golden shiner larvae predation cycle (MANOVA, Wilks lambda, $F = 5.328$, $P < 0.001$, $df = 20$). Swimming

TABLE 1. Measures of each component of the search cycle for three size classes of golden shiner larvae. Size class 1 = 6.22 ± 0.24 mm TL; size class 2 = 8.44 ± 0.22 mm TL; size class 3 = 21.4 ± 0.90 mm TL.

Variable	Fish size class	Mean	SE	<i>n</i>
Unsuccessful search time(s)	1	0.27	0.03	15
	2	0.06	0.01	15
	3	0.31	0.07	15
Move distance (mm)	1	0.34	0.05	30
	2	0.72	0.04	30
	3	0.76	0.11	30
Move time(s)	1	0.21	0.02	15
	2	0.44	0.01	15
	3	0.34	0.08	15
Move speed ($\text{mm}\cdot\text{s}^{-1}$)	1	13.5	2.2	15
	2	18.7	0.8	15
	3	27.5	4.6	15
Move angle (degrees)	1	49.18	4.99	30
	2	34.00	4.85	30
	3	76.57	5.84	30
Successful search time(s)	1	0.13	0.03	10
	2	0.18	0.05	12
	3	0.34	0.09	15
Pursuit distance (mm)	1	0.44	0.06	10
	2	0.63	0.07	12
	3	1.11	0.18	15
Pursuit time(s)	1	1.04	0.12	10
	2	1.11	0.10	12
	3	0.71	0.10	15
Pursuit speed ($\text{mm}\cdot\text{s}^{-1}$)	1	4.6	0.7	10
	2	5.9	0.6	12
	3	15.9	1.3	15
Pursuit angle (degrees)	1	40.70	6.87	10
	2	40.42	6.84	12
	3	40.13	6.74	15

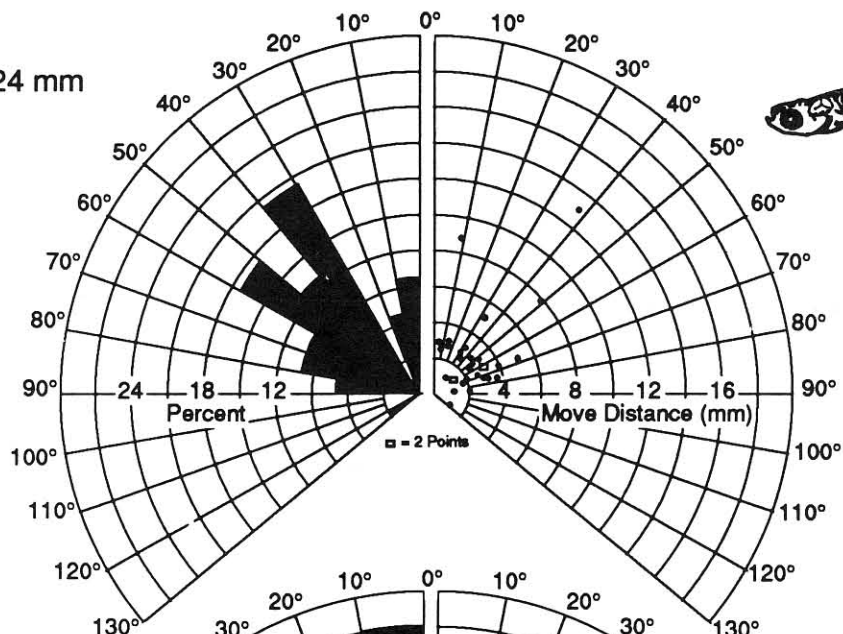
TABLE 2. Summary of the univariate *F*-tests (2,34 df), produced from the multivariate analysis of variance, testing for the effect of fish size on each component of the golden shiner larvae predation cycle.

Variable	<i>F</i> -value	Significance of <i>F</i> -value
Unsuccessful search time	7.367	0.002
Move distance	4.742	0.015
Move time	2.621	0.087
Move speed	6.847	0.003
Move angle	16.591	<0.001
Successful search time	2.267	0.119
Pursuit distance	6.554	0.004
Pursuit time	4.590	0.017
Pursuit speed	37.996	<0.001
Pursuit angle	0.0017	0.998

(move) speed increased with fish size (Tables 1 and 2). Mean move distance was greater for the two larger size classes of larvae than for the smallest size class (Tables 1 and 2; Fig. 2). The duration of move pauses (USST) was shorter in the second larval size class than in the other two (Tables 1 and 2). Mean move angle was greatest for the largest size class (Tables 1 and 2) and the distribution of move angles appeared to skew towards larger angles as the fish got larger (Fig. 2).

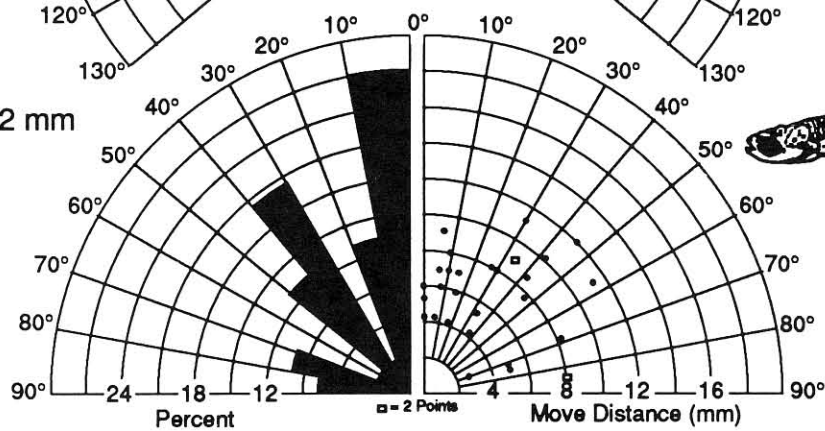
$\bar{X}TL = 6.22 \pm 0.24$ mm

n = 30



$\bar{X}TL = 8.44 \pm 0.22$ mm

n = 30



$\bar{X}TL = 21.4 \pm 0.9$ mm

n = 30

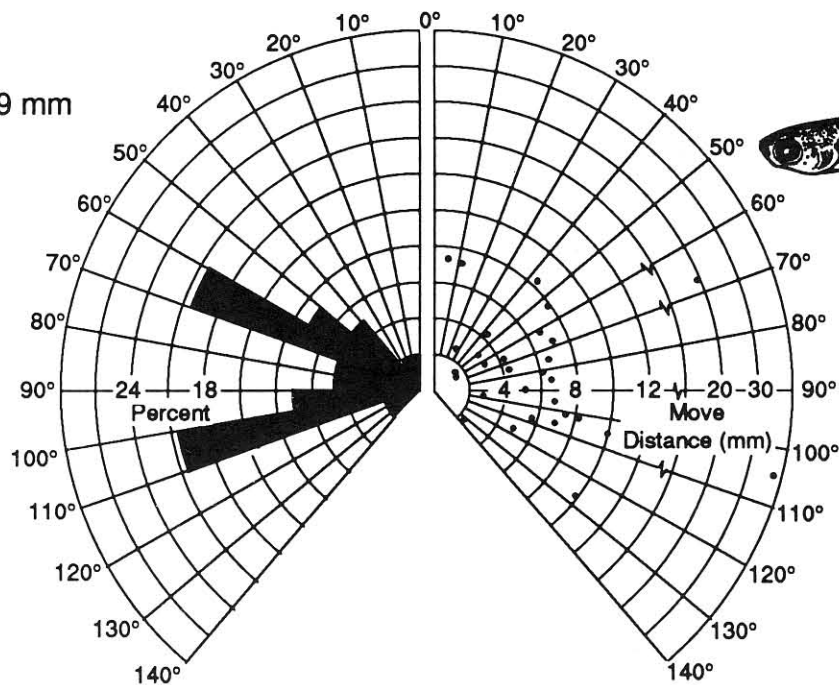
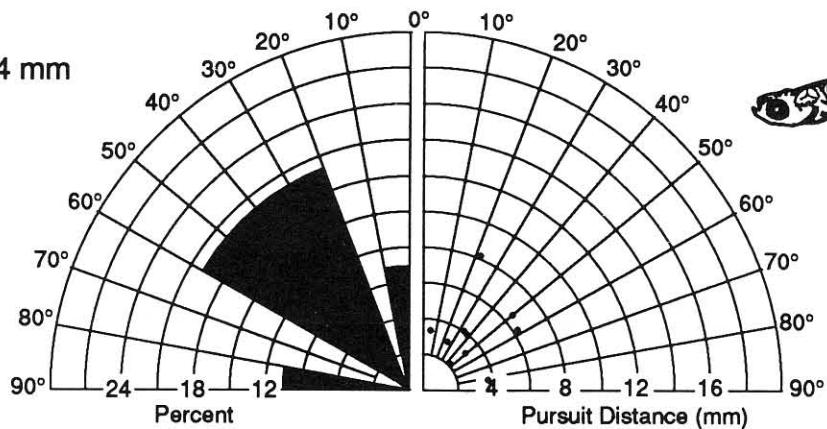


FIG. 2. Move distances and angles (both left- and right-directed) for each of three size classes of golden shiner larvae. Distances are plotted on the right and the percent frequency of locations in each 10° increment of the horizontal visual field is plotted on the left. The points are plotted as if the fish's eyes were positioned in the centre of the polar projection.

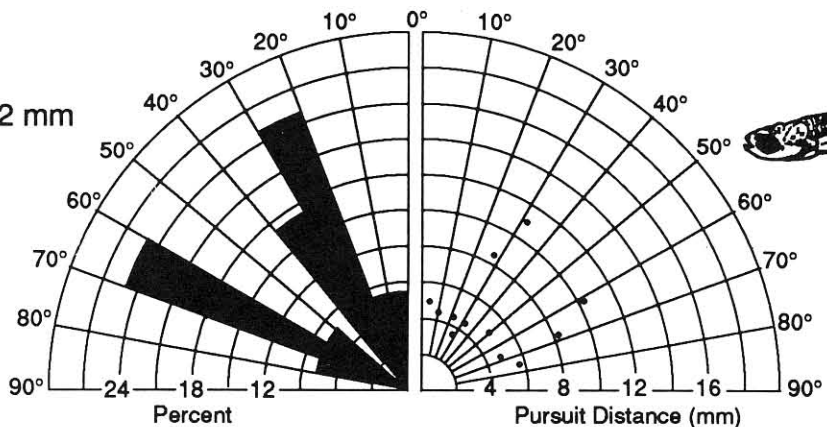
$\bar{X}TL = 6.22 \pm 0.24$ mm

n = 10



$\bar{X}TL = 8.44 \pm 0.22$ mm

n = 12



$\bar{X}TL = 21.4 \pm 0.9$ mm

n = 15

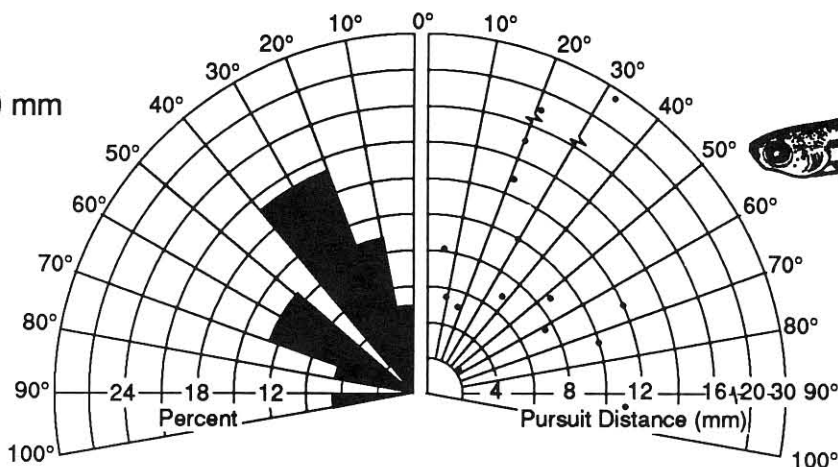


FIG. 3. Pursuit distances and angles (both left- and right-directed) for each of three size classes of golden shiner larvae. Distances are plotted on the right and the percent frequency of locations in each 10° increment of the horizontal visual field is plotted on the left. The points are plotted as if the fish's eyes were positioned in the centre of the polar projection.

Golden shiner larvae typically turned toward a located prey item and approached it by means of rapid tail beats. As they came very near to the prey, they braked using the pectoral fins and sucked the prey into their mouths by rapid expansion of the buccal cavity. No S-posture-type attacks were observed. Pursuit distances increased significantly with fish size (Tables 1 and 2; Fig. 3). The mean values for the duration of location pauses (SST) increased with fish size (Table 1), but these differences were not statistically discernible (Table 2). There was

no discernible relationship between mean pursuit angle and fish size (Tables 1 and 2), although the range of pursuit angles appears to have increased (Fig. 3). Pursuit speeds increased with fish size (Tables 1 and 2).

Discussion

Foraging Behaviour of Golden Shiner Larvae

Although the larvae of several fish species employ an S-posture in attacks on prey (e.g. Hunter 1972; Drost 1987;

Browman and O'Brien 1992), golden shiner larvae did not. Rather, shiner larvae feeding strikes were incorporated into more typical swimming movements, as is true for juvenile zooplanktivorous fish.

Recently, facultative switching of foraging modes has been reported in juvenile golden shiner (Ehlinger 1989b). Juvenile shiner are visually guided particulate-feeders when feeding on large prey and switch to a pump filter-feeding mode, during which their movements are apparently not visually guided, when feeding on high densities of small zooplankton. Further, when particulate-feeding, juvenile shiner were reported to wait 5–10 captures before pausing to swallow the accumulated bolus of prey (Ehlinger 1989b). We did not observe this behaviour, nor pump filter-feeding, perhaps because the prey that we used in our experiments were large relative to the shiner larvae themselves.

Search Strategy of Golden Shiner Larvae

The size-related changes in the components of the golden shiner predation cycle that we observed are similar to those reported for herring, anchovy, and other centrarchids and cyprinids (Hunter 1980; Brown and Colgan 1985; Blaxter 1986; Noakes and Godin 1988). For example, swimming and pursuit speeds and prey pursuit (or reaction) distances increased with fish size in the three species of cyprinids observed by Wanzenböck and Schiemer (1989), as is the case for other species and for golden shiner larvae. Although such size-related changes in foraging behaviour have been reported for many fish species, these parameters have only recently been interpreted with the goal of determining the fish's search strategy (Browman and O'Brien 1992). In the sections that follow, we examine the behavioural characteristics of each component of the golden shiner larvae predation cycle and compare them with those that would be exhibited by a saltatory searcher.

Do Shiner Larvae Search Only While Stationary?

Saltatory searchers scan for prey only during the frequent stationary pauses between repositioning movements (O'Brien et al. 1986, 1989). Several lines of evidence support this interpretation (see O'Brien et al. 1990).

A characteristic distinguishing saltatory from cruise or ambush foragers is the distribution of pursuits within the search space. Assuming that they simultaneously scan the entire search space, both cruise and ambush searchers would be expected to pursue prey at the boundary of the search space. Saltatory-searching white crappie larvae and juveniles pursue prey throughout the search space (O'Brien et al. 1986, 1989; Browman and O'Brien 1992). So do golden shiner larvae (Fig. 3).

Pauses between swimming movements may have functions other than search, e.g. time to orient toward a prey located while swimming or to initiate the attack phase of the predation cycle. If either of these were the case, all or most pauses would be followed by attacks on prey. This is never the case. Only 10–25% of all pauses by white crappie juveniles are followed by attacks on prey (O'Brien et al. 1986). For white crappie larvae, this figure is 1–10% (Browman and O'Brien 1992), as is the case for golden shiner larvae. Further, in every case in which prey were located, orientation toward it did not occur during the stationary pause, but immediately after it, while the fish was engaged in its pursuit of the prey item. Although it is impossible to exclude other possibilities, these observations are consistent with the saltatory-search hypothesis and we conclude that golden shiner larvae search for prey only while stationary.

Drost and van den Boogaart (1986) reported that carp (*Cyprinus carpio*) larvae punctuate their swimming movements with periods of rest that average 0.3 s. The duration of these "rest" periods is similar to the stationary search times reported here for shiner larvae and elsewhere for white crappie larvae (Browman and O'Brien 1992). We suggest that such commonly observed stationary periods, which have been interpreted as times of rest, may in some cases be associated with prey search.

Relationship between Movement Pattern and Search Space Geometry

Animals project what can be termed a scan space while foraging. The geometry of this space is species specific and plastic, varying with environmental conditions and prey type (O'Brien 1979; Dunbrack and Dill 1984; Evans and O'Brien 1988; O'Brien et al. 1989; Bell 1990). For saltatory-searching fish, which are not searching while moving, swimming movements between stationary pauses serve only to bring the animal into a volume of water that has, for the most part, not previously been scanned. If this is indeed the case, there should be a relationship between the distance and angle traveled in repositioning moves and the geometry of the space previously scanned. For example, if after an unsuccessful search an animal moves only a small distance relative to the maximum distance to which it can locate prey, much of its search volume will be scanned again (see O'Brien et al. 1989). Similarly, at least when prey are abundant, it would be energetically wasteful for an animal to move a distance that would take it far beyond the search space it had just scanned.

Turning after a stationary pause is another way saltatory searchers can quickly move into unsearched areas. To benefit from turning (in terms of yield of unsearched space), a saltatory-searching fish must make wider turns in response to larger pursuit angles (O'Brien et al. 1990).

For golden shiner larvae, maximum pursuit distance increased with fish size and, on average, move distances were slightly shorter (Table 1; Fig. 2 and 3). Further, most pursuits occurred at angles of 20–60° from forward-directed (Fig. 3); there is a pronounced lack of pursuits in the first 0–20° of the search space. The distribution of move angles is similar (Fig. 2), indicating that golden shiner larvae modulate their swimming movements in the same manner as do other saltatory searchers, i.e. to minimize redundant search efforts (O'Brien et al. 1989).

Conclusions and General Considerations

Our results indicate that at least some fish larvae are not cruise searchers. Rather, the search pattern employed by golden shiner larvae, and that of white crappie larvae (Browman and O'Brien 1992), is much like the saltatory-search strategy that we have described for juvenile zooplanktivores. Further, in recent experiments, one of us (Browman) has observed similar search patterns in Atlantic cod (*Gadus morhua*) larvae.

Accurate characterization of a fish's search pattern is important for measuring and interpreting, among other things, predatory-prey encounter frequencies, prey choice and dietary preferences, and the efficiency of movement patterns associated with foraging. For example, virtually all characterizations of search strategies in fish larvae imply that they are cruise searchers (e.g. Rosenthal and Hempel 1970; Hunter 1972; Wanzenböck and Schiemer 1989; Arnold and Holford 1990). Specific examples include the description of herring larvae as "tube searchers" that swim through the water projecting a tube-

shaped search space (Rosenthal 1969; Rosenthal and Hempel 1970). This characterization implies cruise search. Similarly, plaice (*Pseudopleuronectes platessa*) larvae have been described as projecting an elliptical search space as they swim through the water column (Arnold and Holford 1990). Further, in simulation models of foraging in fish larvae, it is common practice to calculate search rate (or the volume of water scanned) as the product of mean (continuous) swimming speed and the cross-sectional area of the perceptual field (e.g. Wanzenböck and Schiemer 1989; Arnold and Holford 1990; also see review in Blaxter 1986). These search rates, along with estimates of prey abundance, are used to establish prey encounter rates for the larvae. Such calculations assume that the fish is searching continuously as it swims: a cruise search strategy is implied.

For a saltatory-searching fish, which searches only while stationary, the calculation of prey encounter rate described above will not accurately reflect the true rate. Rather, it is the mean duration of the stationary periods that punctuate swimming movements and their frequency that should be used to estimate search time. Using a simulation model currently under development, we are quantitatively evaluating differences between pause-travel and cruise search interpretations of search patterns in fish larvae.

Acknowledgments

This work was supported by NSF grant BSR-8717454 and University of Kansas Biomedical and General Research Fund grants to W.J.O. H.I.B. was supported by a postgraduate scholarship from the Natural Sciences and Engineering Research Council of Canada, by a bursary from the Quebec Ministry of Higher Education and Science, and, during manuscript preparation, by an E. B. Eastburn postdoctoral fellowship from the Hamilton Foundation of Canada. We thank I. Bernard for helping with the videotape analysis, J. Atwater for his assistance with the statistical analysis, and J. Racy, Manager of the Kaw Valley Fish Farm, for supplying golden shiner eggs.

References

ARNOLD, G. P., AND B. H. HOLFORD. 1990. The reactive perceptual field of the larval plaice (*Pleuronectes platessa* L.): a three-dimensional analysis of visual feeding. *Rapp. P.-V. Comm. Int. Explor. Mer* 191: 474.

ARNOLD, G. P., AND P. B. N. NUTTALL-SMITH. 1974. Shadow cinematography of fish larvae. *Mar. Biol.* 28: 51–53.

AUER, N. A. 1982. [ED.] Identification of larval fishes of the great lakes basin with special reference to the lake Michigan drainage. *Great Lakes Fish. Comm. Spec. Publ.* 82-3.

BELL, W. J. 1990. Searching behaviour. The behavioural ecology of finding resources. Chapman and Hall, New York, NY. 400 p.

BLAXTER, J. H. S. 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Trans. Am. Fish. Soc.* 115: 98–114.

BROWMAN, H. I., AND W. J. O'BRIEN. 1992. The ontogeny of prey search behaviour in the white crappie, *Pomoxis annularis*. *Environ. Biol. Fishes* 34. (In press)

BROWN, J. A., AND P. W. COLGAN. 1984. The ontogeny of feeding behaviour in four species of centrarchid fish. *Behav. Process* 9: 395–411.

1985. Interspecific differences in the ontogeny of feeding behavior in two species of centrarchid fish. *Z. Tierpsychol.* 70: 70–80.

DROST, M. R. 1987. Relation between aiming and catch success in larval fishes. *Can. J. Fish. Aquat. Sci.* 44: 304–315.

DROST, M. R., AND J. G. M. VAN DEN BOOGAART. 1986. The energetics of feeding strikes in larval carp, *Cyprinus carpio*. *J. Fish. Biol.* 29: 371–379.

DUNBRACK, R. L., AND L. M. DILL. 1984. Three-dimensional prey reaction field of the juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 41: 1176–1182.

EHLINGER, T. J. 1989a. Learning and individual variation in bluegill foraging: habitat-specific techniques. *Anim. Behav.* 38: 643–658.

1989b. Foraging mode switches in the golden shiner (*Notemigonus crysoleucas*). *Can. J. Fish. Aquat. Sci.* 46: 1250–1254.

1990. Habitat choice and phenotypic-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. *Ecology* 71: 886–896.

EHLINGER, T. J., AND D. S. WILSON. 1988. Complex foraging polymorphism in bluegill sunfish. *Proc. Natl. Acad. Sci. USA* 85: 1878–1882.

EVANS, B. I., AND W. J. O'BRIEN. 1988. A reevaluation of the search cycle of planktivorous Arctic grayling, *Thymallus arcticus*. *Can. J. Fish. Aquat. Sci.* 45: 187–192.

HALL, D. J., AND T. J. EHLINGER. 1989. Perturbation, planktivory, and pelagic community structure: the consequence of winterkill in a small lake. *Can. J. Fish. Aquat. Sci.* 46: 2203–2209.

HALL, D. J., E. E. WERNER, J. F. GILIAM, G. G. MITTELBACH, D. HOWARD, AND C. G. DONER. 1979. Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). *J. Fish. Res. Board Can.* 36: 1029–1039.

HATCH, J. T. 1988. Ontogenetic shifts in feeding habits of mixed cohort schools of larval golden shiners. *Verh. Int. Ver. Limnol.* 23: 1704–1709.

HUNTER, J. R. 1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. *Fish. Bull. U.S.* 70: 821–838.

1980. The feeding behavior and ecology of marine fish larvae, p. 287–330. In J. E. Bardach, J. J. Magnuson, R. C. May, and J. M. Reinhart [ed.] *Fish behavior and its use in the capture and culture of fishes*. ICLARM Conf. Proc. 5, Manila.

JANSSEN, J. 1982. Comparison of searching behavior for zooplankton in an obligate planktivore, blueback herring (*Alosa aestivalis*) and a facultative planktivore, bluegill (*Lepomis macrochirus*). *Can. J. Fish. Aquat. Sci.* 39: 1649–1654.

JOHANNES, M. R. S., D. J. MCQUEEN, T. J. STEWART, AND J. R. POST. 1989. Golden shiner (*Notemigonus crysoleucas*) population abundance: correlations with food and predators. *Can. J. Fish. Aquat. Sci.* 46: 810–817.

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. Fishes* 5: 305–314.

1985. The piscivore feeding guild of fishes in small freshwater ecosystems. *Environ. Biol. Fishes* 12: 119–129.

LAZZARO, X. 1987. A review of planktivorous fish: their evolution, feeding behaviors, selectivities, and impacts. *Hydrobiologia* 146: 97–167.

MCLAUGHLIN, R. L. 1989. Search modes of birds and lizards: evidence for alternative movement patterns. *Am. Nat.* 133: 654–670.

NOAKES, D. L. G., AND J.-G. J. GODIN. 1988. Ontogeny of behavior and concurrent developmental changes in sensory systems in teleost fishes, p. 345–395. In W. S. Hoar and D. J. Randall [ed.] *Fish physiology*. Vol. XIB. Viviparity and post hatching juveniles. Academic Press, New York, NY.

O'BRIEN, W. J. 1979. The predator-prey interactions of planktivorous fish and zooplankton. *Am. Sci.* 67: 572–581.

O'BRIEN, W. J., H. I. BROWMAN, AND B. I. EVANS. 1990. Search strategies in foraging animals. *Am. Sci.* 78: 152–160.

O'BRIEN, W. J., B. I. EVANS, AND H. I. BROWMAN. 1989. Flexible search tactics and efficient foraging in saltatory searching animals. *Oecologia* 80: 100–110.

O'BRIEN, W. J., B. I. EVANS, AND G. HOWICK. 1986. A new view of the predation cycle in a planktivorous fish. *Can. J. Fish. Aquat. Sci.* 43: 1894–1899.

ROSENTHAL, H. 1969. Investigations regarding the prey catching behavior in larvae of the herring (*Clupea harengus*). *Mar. Biol.* 3: 208–221.

ROSENTHAL, H., AND G. HEMPEL. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.), p. 344–364. In J. H. Steele [ed.] *Marine food chains*. Oliver & Boyd, Edinburgh.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. *Freshwater fishes of Canada*. Bull. Fish. Res. Board Can. 184: 966 p.

SINCLAIR, M. 1988. *Marine populations. An essay on population regulation and speciation*. Washington Sea Grant Program and University of Washington Press, Seattle, WA.

STATISTICAL PACKAGE FOR THE SOCIAL SCIENCES. 1987. SPSS/PC+ advanced statistics guide v2.0. McGraw Hill Book Company, New York, NY.

TYE, A. 1989. A model of search behaviour for the northern wheatear *Oenanthe oenanthe* (Aves, Turdidae) and other pause-travel predators. *Ethology* 83: 1–18.

WANZENBÖCK, J., AND F. SCHIEMER. 1989. Prey detection in cyprinids during early development. *Can. J. Fish. Aquat. Sci.* 46: 995–1001.

WETTERER, J. K. 1989. Mechanisms of prey choice by planktivorous fish: perceptual constraints and rules of thumb. *Anim. Behav.* 37: 955–967.