

# The ontogeny of search behavior in the white crappie, *Pomoxis annularis*

Howard I. Browman<sup>1</sup> & W. John O'Brien

*Department of Systematics and Ecology, The University of Kansas, Lawrence, KS 66045-2106, U.S.A.*

<sup>1</sup> *Present address: Department of Biology, University of Victoria, P.O. Box 1700, Victoria, British Columbia V8W 2Y2, Canada*

Received 13.8.1990

Accepted 13.5.1991

**Key words:** Teleost fish, Foraging behavior, Zooplanktivory, Pause-travel search, Saltatory search, Locomotory pattern, Prey encounter rate

## Synopsis

Animals that forage for discrete, isolated resources are often characterized as either 'ambush' (sit-and-wait) or 'cruise' (active) searchers. Juvenile white crappie, *Pomoxis annularis*, search for zooplankton prey using a saltatory search (SS) strategy. Unlike ambush and cruise search, SS involves scanning for prey only during the brief stationary periods that punctuate repositioning movements. If prey are not found, these fish swim a short distance, stop, and scan again. In this paper, we describe the ontogeny of prey search in the white crappie and compare the search pattern that they employ with that of juveniles. White crappie larvae searched for prey throughout the search space and only during the pauses that punctuated swimming movements. Prey location distances increased with fish size, as did several other components of the predation cycle. We conclude that white crappie larvae employ a search strategy similar to that exhibited by juveniles. We emphasize that, to obtain an accurate assessment of the feeding ecology of early life history stages, the search pattern that they employ must be characterized, and its components quantified.

## Introduction

The larvae of many fish species are visually guided zooplanktivorous predators and their foraging behavior has been studied extensively (Hunter 1980, Blaxter 1986, Noakes & Godin 1988). Ontogenetic changes in specific aspects of foraging behavior have been investigated: for example, a fish's ability to locate and capture prey improves markedly and rapidly during ontogeny (Blaxter 1986, Drost 1987, Meyer 1986, 1987, Noakes & Godin 1988, Wanzenböck & Schiemer 1989, Wanzenböck 1992). However, ontogenetic changes in the prey search strategies of fish larvae, and how these relate to those of juveniles and adults, have not been explored.

Animals that forage for discrete, isolated resources, such as zooplanktivorous fish larvae, are generally characterized as either 'ambush' (sit-and-wait) or 'cruise' (active) searchers (Schoener 1971, Huey & Pianka 1981, McLaughlin 1989, Bell 1990, O'Brien et al. 1990). Ambush foragers move infrequently, and search for prey at the periphery of their strike range, waiting for prey to cross into it before attacking. Cruise foragers move more-or-less continuously and scan for prey at the outer boundary of their search space. An intermediate search strategy, termed 'saltatory' search by O'Brien et al. (1989, 1990), and 'pause-travel' search by Tye (1989), has recently been described in several species of zooplanktivorous fishes and in several other taxonomic groups (see Andersson

1981, Janssen 1982, Ehlinger & Wilson 1988, Ehlinger 1989, 1990, Tye 1989, 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 repositioning movements. If prey are not located, the animal moves a short distance, stops, and scans again (O'Brien et al. 1986, 1989, 1990, Evans & O'Brien 1988, Tye 1989).

Zooplanktivorous juveniles of the white crappie, *Pomoxis annularis*, are saltatory searchers; they search briefly while stationary and, if they do not locate a prey, swim a short distance before stopping to scan again (O'Brien et al. 1986, 1989, 1990). In this paper, we report on the development of foraging behavior in white crappie larvae, compare it to the search strategy of juveniles, and discuss how accurate search strategy characterizations are essential in assessments of the feeding ecology of early life history stages.

## Materials and methods

### *Study species*

White crappie are approximately 3–4 mm in length at hatching and growth in the first several days is rapid (Browman 1989). Fish < 16 mm TL are considered larvae, while individuals of 16–27 mm TL are considered juveniles (Auer 1982). White crappie are zooplanktivorous until 12–15 cm TL, after which they are almost exclusively piscivorous (Marcy 1954, O'Brien et al. 1984, Heidinger et al. 1985). Smaller individuals (< 12–15 cm TL) forage in the pelagic zones of warm water lakes and reservoirs throughout North America. The species is a littoral zone nest spawner (Scott & Crossman 1973).

### *General procedures*

Adult white crappie were collected using fyke nets in late May and early June 1988 from Clinton Lake, a reservoir 4 km west of Lawrence, Kansas. Eight pairs of ripe adults were collected on each of three

dates. Four pairs were placed in each of two 450 l indoor holding tanks. The tanks had gravel-covered bottoms and were supplied with filtered and UV sterilized water. Water temperature was maintained at 20°C in a climate-controlled room on a 14L : 10D cycle. One or more adult pairs spawned during their first night in captivity. Adults were kept with the eggs for two days to allow paternal fanning of the embryos. Embryos hatched 2–3 days after fertilization. Eleutheroembryos were  $2.74 \pm 0.04$  mm long ( $\bar{x}$  TL  $\pm$  SD,  $N = 5$ ). Prey items were first observed in the gut on day 9 after hatching. These fish were  $4.49 \pm 0.08$  mm in length ( $N = 5$ ).

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

### *Experimental protocol*

In order to evaluate size-related changes in search patterns, experiments were conducted on an ontogenetic series of fish. Observations began when food was first observed in the gut. First-feeding fish were  $4.47 \pm 0.22$  mm ( $N = 5$ ). The mean total lengths ( $\pm$  SD,  $N = 5$ ) of fish observed in later experiments were:  $7.31 \pm 0.27$  mm,  $9.03 \pm 0.69$  mm,  $12.07 \pm 0.33$  mm,  $14.37 \pm 0.33$  mm, and  $19.61 \pm 1.41$  mm. The largest fish observed were 56 days post-hatch. According to the criteria summarized in Auer (1982), two of the five fish in the 19.61 mm size class were recently transformed juveniles. When larvae reached 9 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, three fish were placed in a  $30 \times 30 \times 30$  cm 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 lux ( $\pm 10$ ) and water temperature was 20°C.

At the beginning of an experiment, food items

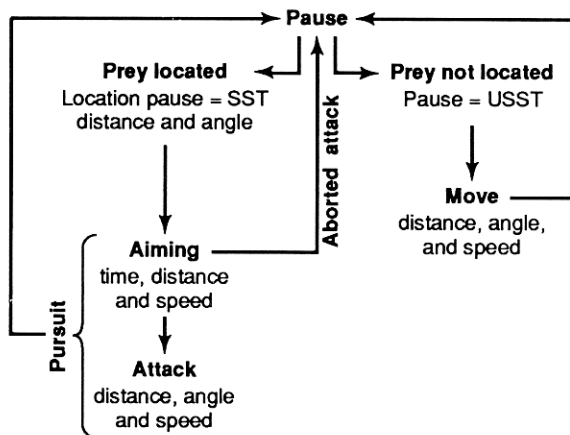
(<100  $\mu\text{m}$  size-class) were introduced into the observation aquarium at an abundance of 100 prey  $\text{l}^{-1}$ . No clumping of prey was visible on the video tapes. Prey consisted of copepod nauplii or early copepodites for fish <15 mm. White crappie larvae feed almost exclusively on these items in the wild (Marcy 1954, Mathur & Robbins 1971). *Artemia* nauplii were included for fish >15 mm. Total prey abundance remained 100  $\text{l}^{-1}$ . 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 items  $\text{l}^{-1}$  in the 12 l observation tank. In each experiment, foraging behavior was videotaped until the three fish had attempted at least 15 attacks on prey. All experiments were conducted between 1100 and 1300 h.

#### *Observations and analysis of foraging and search behavior*

Silhouette video photography was used to record the behavior of crappie larvae (Arnold & Nutall-Smith 1974, Edgerton 1977). This method has several advantages over standard cinagraphic or video techniques. First, it can be used to make detailed observations of small transparent organisms such as fish larvae (e.g. Hunter 1972, Drost 1987, Arnold & Holford 1990). Second, events can be filmed in a large depth of field (approximately 15 cm) with a relatively large field of view (18 cm); free-swimming predators and their prey can be observed under laboratory conditions. Third, magnification is independent of distance from the camera, and the resolution of the system is extremely good; objects as small as 0.2 mm in diameter can be resolved. The system used here is described in detail elsewhere (Browman et al. 1989).

The videotapes were analyzed frame-by-frame on a video monitor using a Panasonic AG-1950 video tape machine. All time intervals were measured in increments of 0.033 sec. For each experiment, a videotaped ruler established conversions from monitor units to millimeters. Sequences in which movement in the vertical plane exceeded

#### a) Search cycle of white crappie larvae



#### b) Search cycle of white crappie juveniles

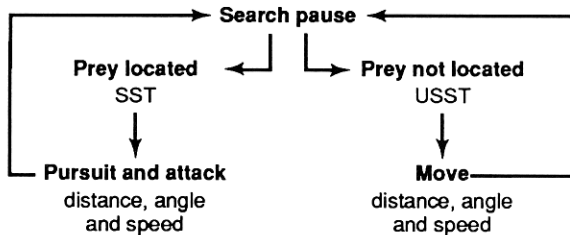


Fig. 1. The predation cycles for (a) white crappie larvae, and (b) juveniles. The primary differences are the presence of a pronounced aiming sequence and the possibility for aborted attacks in the larva's cycle.

5° from horizontal were not analyzed (approximately 5% of all sequences).

Search behavior was analyzed by assigning the activities of the fish to one of the components of their predation cycle: pause, move (swim), pursuit (aiming), or attack (Fig. 1). 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 (determined a posteriori) and the posi-

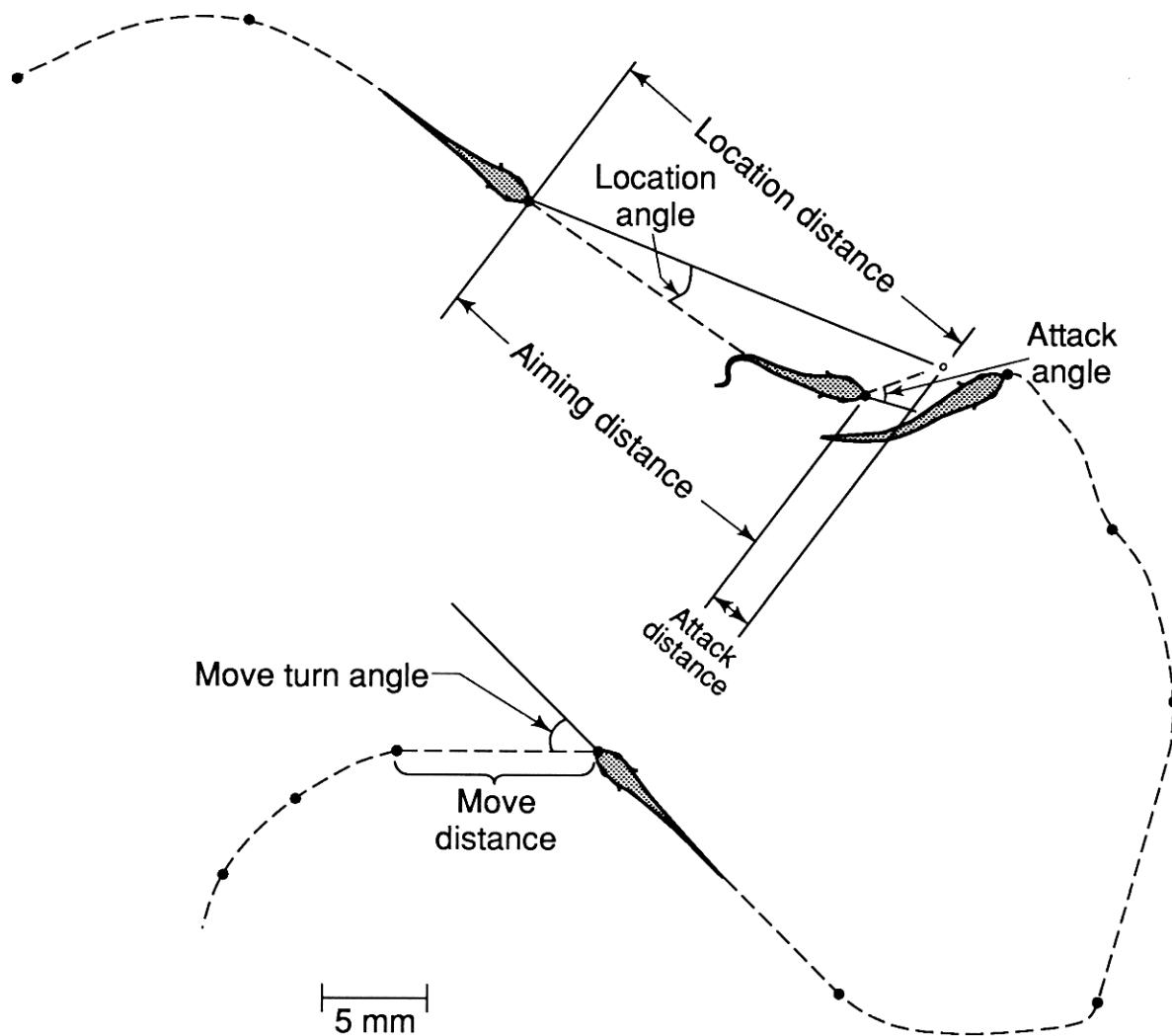


Fig. 2. A typical search path and attack sequence for white crappie larvae, sketched directly off of the television screen, illustrating the measurements drawn from it. The solid dots along the dashed line (the path of motion) represent stationary pauses, the open dot a prey item.

tion of the prey itself, is the location distance. Once located, crappie larvae move slowly towards their prey before assuming an attack posture (described below). The distance from the point at which a prey item is first located to the point at which the attack posture is assumed is the aiming distance (Fig. 2). The distance from the tip of the snout just prior to the lunging attack on a prey item is the attack distance.

Move, location, aiming, and attack distances and angles were marked on the monitor with a grease

pencil and measured. The longitudinal body axis of the fish was defined as the central axis of the forward-directed visual field (i.e.  $0^\circ$  from forward-directed). Location 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 a posteriori as the point at which the fish attacked the prey item, or directly when the prey item could be seen on the screen). Attack angles and distances were determined in an analogous manner (Fig. 2). 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. The duration of these events, as well as that of stationary pauses between them, were also measured. Move, aiming and attack speeds were calculated from these measurements. The number of aborted attacks, in which a fish assumed the attack posture but did not follow through with it, were also enumerated.

A multivariate analysis of variance, with a repeated measures design (SPSS/PC +, routine MANOVA), was used to test for the overall effect of fish size on all of the components of the predation cycle (Barker & Barker 1984, SPSS/PC + Advanced Statistics Guide 1987). All MANOVA parametric assumptions were tested for and met. The univariate F-tests calculated from the MANOVA were used to evaluate whether fish size had an effect on any individual component of the predation cycle.

Since the data were categorical, size-related trends in the components of the predation cycle were evaluated using discriminant functions analysis (SPSS/PC +, routine DISCRIMINANT). Discriminant functions analysis attempts to separate populations (here fish of different sizes) using some

combination of the variables observed. In discriminant analysis, a linear combination of the independent variables (the components of the search cycle) is formed and serves as the basis for assigning cases to groups (fish size). The linear discriminant equations produced are similar to multiple linear regression equations (Lachenbruch 1975, SPSS/PC + Advanced Statistics Guide 1987).

## Results

Fish size had a significant overall effect on the components of the white crappie larvae predation cycle (MANOVA,  $F = 4.773$ ,  $p < 0.001$ ,  $df = 75$ ).

Swimming in crappie larvae was punctuated by frequent pauses (every 1–4 s) and turns (Fig. 2). For larvae  $< 14$  mm, 1–10% of pauses were followed by attacks on prey. For larvae  $> 14$  mm, 10–25% of pauses were followed by attacks on prey.

The entire predation sequence, from prey location to attack, took an average of 2 sec. Its duration did not significantly vary with fish size.

Swimming (move) speed increased significantly with fish size (Table 1, 2, Fig. 3a). Although the

Table 1. Univariate F-tests (5,62df), produced from a multivariate analysis of variance, testing for the effect of fish size on each component of the white crappie larvae predation cycle.

Variable	Hypothesis S.S	Error S.S.	Hypothesis M.S.	Error M.S.	F-Value	Significance of F-value
Location pause (SST)	0.448	3.841	0.090	0.062	1.448	0.22
Location distance	538.602	356.364	107.720	5.748	18.741	$< 0.001$
Location angle	4531.099	27519.648	906.220	443.865	2.042	0.085
Aiming distance	677.887	379.786	135.577	6.126	22.133	$< 0.001$
Aiming time	21.201	34.059	4.240	0.549	7.719	$< 0.001$
Aiming speed	225.126	102.527	45.025	1.654	27.228	$< 0.001$
Attack distance	5.558	15.786	1.112	0.255	4.366	0.002
Attack angle	495.103	6905.614	99.021	111.381	0.889	0.494
Attack time	0.009	0.031	0.002	0.001	3.384	0.009
Attack speed	9015.684	29741.655	1803.137	479.704	3.759	0.005
Move pause (USST)	6.141	19.570	1.228	0.316	3.891	0.004
Move distance	204.684	1470.028	40.937	23.710	1.727	0.142
Move angle	25025.768	32989.685	5005.154	532.092	9.407	$< 0.001$
Move time	99.760	296.052	19.952	4.775	4.178	0.002
Move speed	484.502	782.709	96.900	12.624	7.676	$< 0.001$

largest larvae (19.61 mm) had a greater mean move distance than that for any of the other size classes (Fig. 5), move distance was not affected by larval body size (Table 1, 2). The duration of pauses preceding moves (USST) decreased with fish size (Table 1, 2, Fig. 3b), as did move angle (Table 1, 2, Fig. 5).

Crappie larvae typically turned toward a located prey item and approached it by means of rapid tail beats. Location distances increased significantly with fish size (Table 1, 2, Fig. 6). The duration of pauses preceding pursuits-attacks on prey (SST) tended to decrease with fish size (Fig. 3c), although the trend was not statistically significant (Table 1, 2). There was a negative, although non-significant trend between mean location angle and fish size (Table 1, 2, Fig. 6). The frequency of locations at angles  $> 20^\circ$  from forward-directed decreased with increasing fish size (Fig. 6).

As crappie larvae approach prey their tail ceases to beat and they typically assume a sinuous posture (S-posture). The fish continue to move toward the prey by sculling the pectoral fins and undulating the finfold, while maintaining the S-posture. This closing of distance between the larva and its prey (aiming distance) increased significantly with fish size

(Table 1, 2, Fig. 4a). Swimming speed during aiming also increased significantly with fish size (Table 1, 2, Fig. 4b). Occasionally, and while maintaining the attack posture, larvae moved a short distance (a few mm) backwards to track a prey item.

During aiming, larvae attempted to keep prey directly in front of their snout by making slight adjustments in orientation using the pectoral fins. The direction of attack was related to the laterality of the S-posture. That is, if the S bows to the left, the larva is propelled slightly to the right, and vice versa. In some cases, the laterality of the S-posture was altered by the fish during aiming. This occurred when prey items moved out of range to the side opposite that the tail would have propelled the larva in its original posture.

Larvae did not always follow prey movements and, in such cases, the S-posture was released, sometimes after several changes in its laterality. These events were enumerated as aborted attacks. The proportion of aborted attacks decreased with fish size (Fig. 4c).

When prey were a short distance away (2–4 mm from the snout), larvae opened their mouths and rapidly ( $< 30$  msec) straightened, driving forward through the volume of water containing the prey

Table 2. Summary of discriminant analysis testing for the effect of fish size on the components of the white crappie larvae predation cycle.

Variable	Canonical correlation	Wilks' Lambda	$\chi^2$	df	Significance	Regression equation
Location pause	0.3082	0.9050	7.235	5	0.204	–
Location distance	0.7440	0.4465	60.873	5	$< 0.0001$	Size = $-2.659 + 0.403$ (L distance)
Location angle	0.3628	0.8684	10.654	5	0.059	Size = $-1.382 + 0.494$ (L angle)
Aiming distance	0.7467	0.4424	57.490	5	$< 0.0001$	Size = $-1.655 + 0.328$ (Aim distance)
Aiming time	0.6575	0.5677	39.916	5	$< 0.0001$	Size = $-3.055 + 1.328$ (Aim time)
Aiming speed	0.7206	0.4807	51.637	5	$< 0.0001$	Size = $-1.362 + 0.542$ (Aim speed)
Attack distance	0.5251	0.7243	24.357	5	0.0002	Size = $-4.252 + 1.918$ (Atk distance)
Attack angle	0.2549	0.9350	5.071	5	0.4073	–
Attack time	0.4845	0.7652	17.792	5	0.0032	Size = $-2.227 + 45.566$ (Atk time)
Attack speed	0.4962	0.7538	18.797	5	0.0021	Size = $-2.465 + 0.466$ (Atk speed)
Move pause	0.4865	0.7634	19.036	5	0.0019	Size = $-1.063 + 1.829$ (Move pause)
Move distance	0.3314	0.8902	8.202	5	0.1454	–
Move angle	0.6146	0.6223	33.443	5	$< 0.0001$	Size = $-1.266 + 0.398 \times 10^{-1}$ (Move angle)
Move time	0.5113	0.7386	20.151	5	0.0012	Size = $-0.742 + 0.460$ (Move time)
Move speed	0.6502	0.5773	38.733	5	$< 0.0001$	Size = $-2.000 + 0.286$ (Move speed)

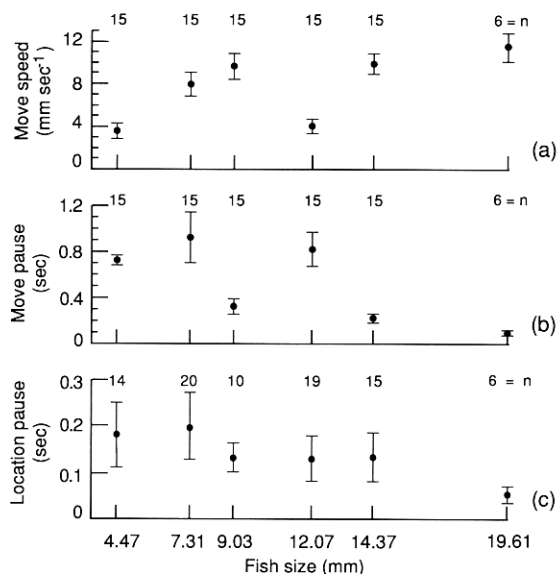


Fig. 3. Size-related changes in (a) move speed, (b) the duration of pauses prior to moves (unsuccessful search time), and (c) the duration of pauses prior to prey locations (successful search time) for white crappie larvae. Error bars represent SE.

item. Attack speeds ranged from 36.42–68.86 mm sec<sup>-1</sup>. All attacks by fish < 14 mm TL were of the S-posture type. Fish > 14 mm assumed a reduced S-posture and used the tail to advance on prey. In 20 mm fish, < 10% of attacks employ the S-posture, and these appeared to be directed at copepods that continuously swam out of the fish's path. In all other attacks, prey were sucked into the fish's buccal cavity.

Attack distance, time, and speed all increased significantly with fish size (Table 1, 2, Fig. 7). There was no significant relationship between attack angle and fish size (Table 1, 2). Only three size classes are presented in Figures 5, 6 and 7 because the distributions of move, location, and prey attack angles and distances were similar for the intermediate size classes. Although the trend was not significant, the range of attack angles decreased with fish size; all attacks on prey by the largest fish (19.61 mm) were straight ahead (Fig. 7).

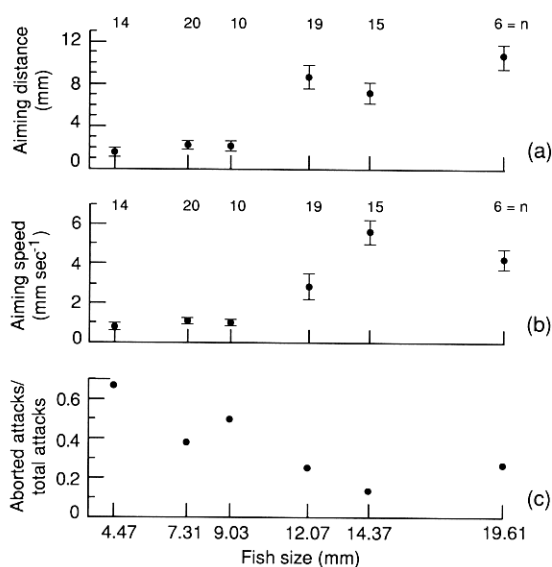


Fig. 4. Size-related changes in (a) aiming distance, (b) aiming speed, and (c) the number of aborted attacks relative to the total number of attacks for white crappie larvae. Error bars represent SE.

## Discussion

### Foraging behavior of white crappie larvae

The sinuous attack posture employed by white crappie larvae is similar to that described for another centrarchid, the black crappie, *Pomoxis nigromaculatus* (Brown & Colgan 1985). Sinuous attack postures have also been reported for northern anchovy larvae, *Engraulis mordax* (Hunter 1972, 1977), herring larvae, *Clupea harengus* (Rosenthal 1969, Rosenthal & Hempel 1970), whitefish larvae, *Coregonus wartmanni* (Braum 1964), northern pike larvae, *Esox lucius* (Braum 1963, Drost 1987), and the larvae of the cichlid, *Cichlasoma managuense* (Meyer 1986, 1987).

White crappie larvae up to approximately 14 mm TL use the sinuous posture exclusively in attacks on prey. Fish of 14–20 mm TL employ both a full (termed 'lunge' by Brown & Colgan 1984) and a reduced S-posture (termed 'snap' by Brown & Colgan 1984). This size range represents the transition from the larval to the juvenile period. The reduced S-posture was employed in attacks on all of the prey types present in our experiments, including

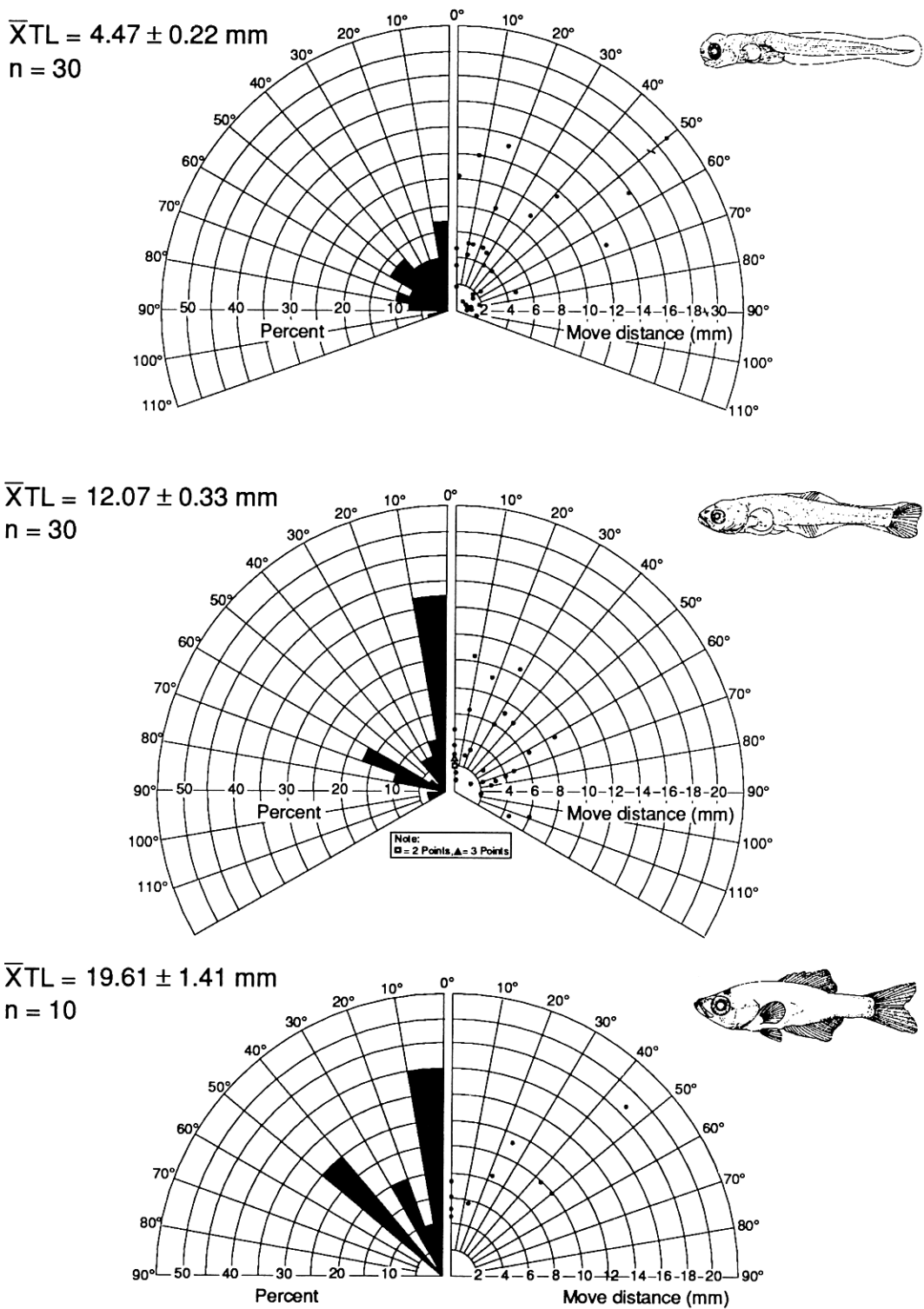


Fig. 5. Size-related changes in move distances (both left- and right-directed) and angles for white crappie larvae are plotted on the right, and the percent frequency of locations in each  $10^\circ$  increment of the horizontal visual field are plotted on the left. The points are plotted as if the fish's eyes were positioned in the centre of the polar projection.



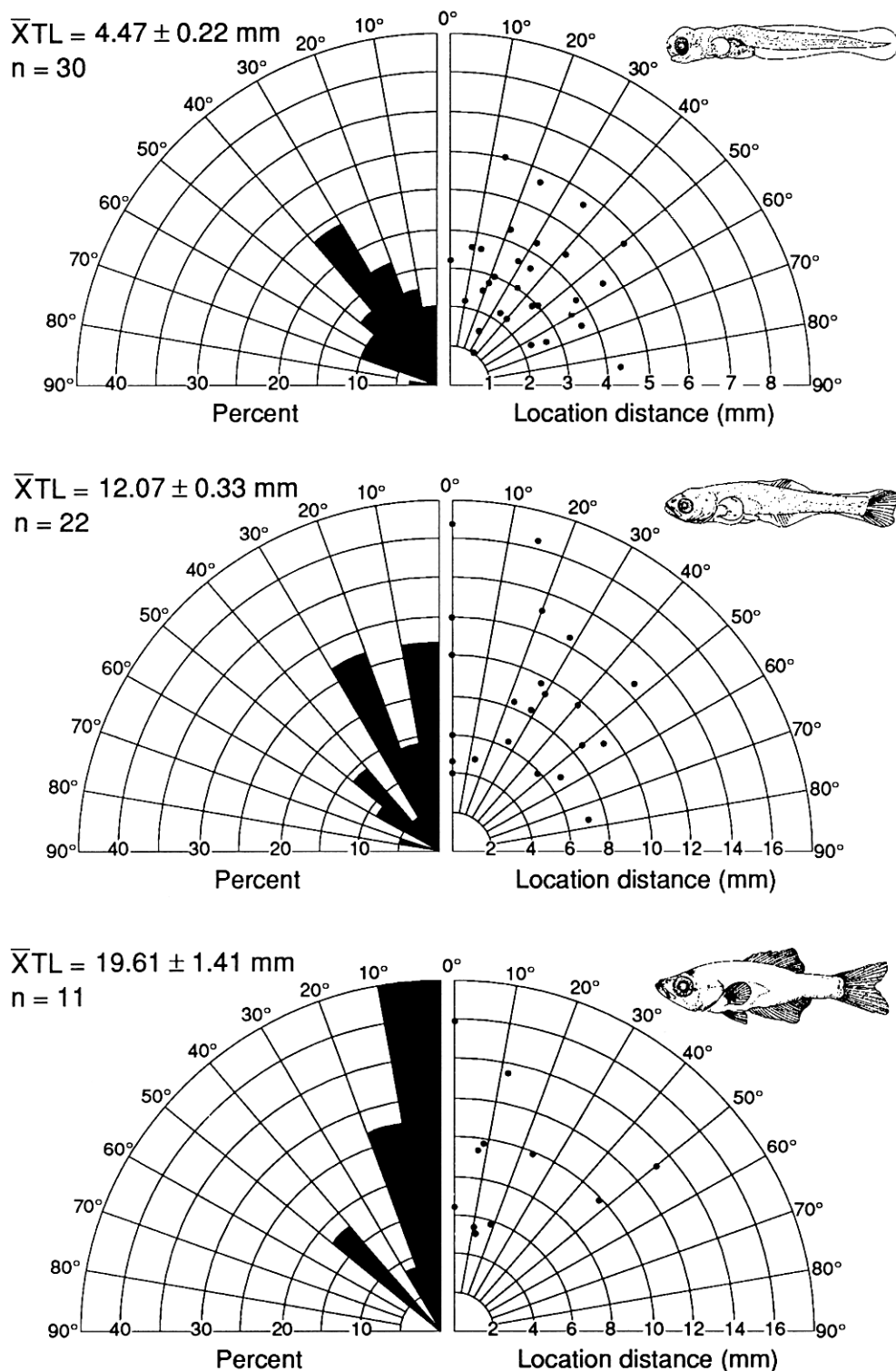


Fig. 6. Size-related changes in location distances (both left and right-directed) and angles for white crappie larvae are plotted on the right, and the percent frequency of locations in each 10° increment of the horizontal visual field are plotted on the left. The points are plotted as if the fish's eyes were positioned in the centre of the polar projection.

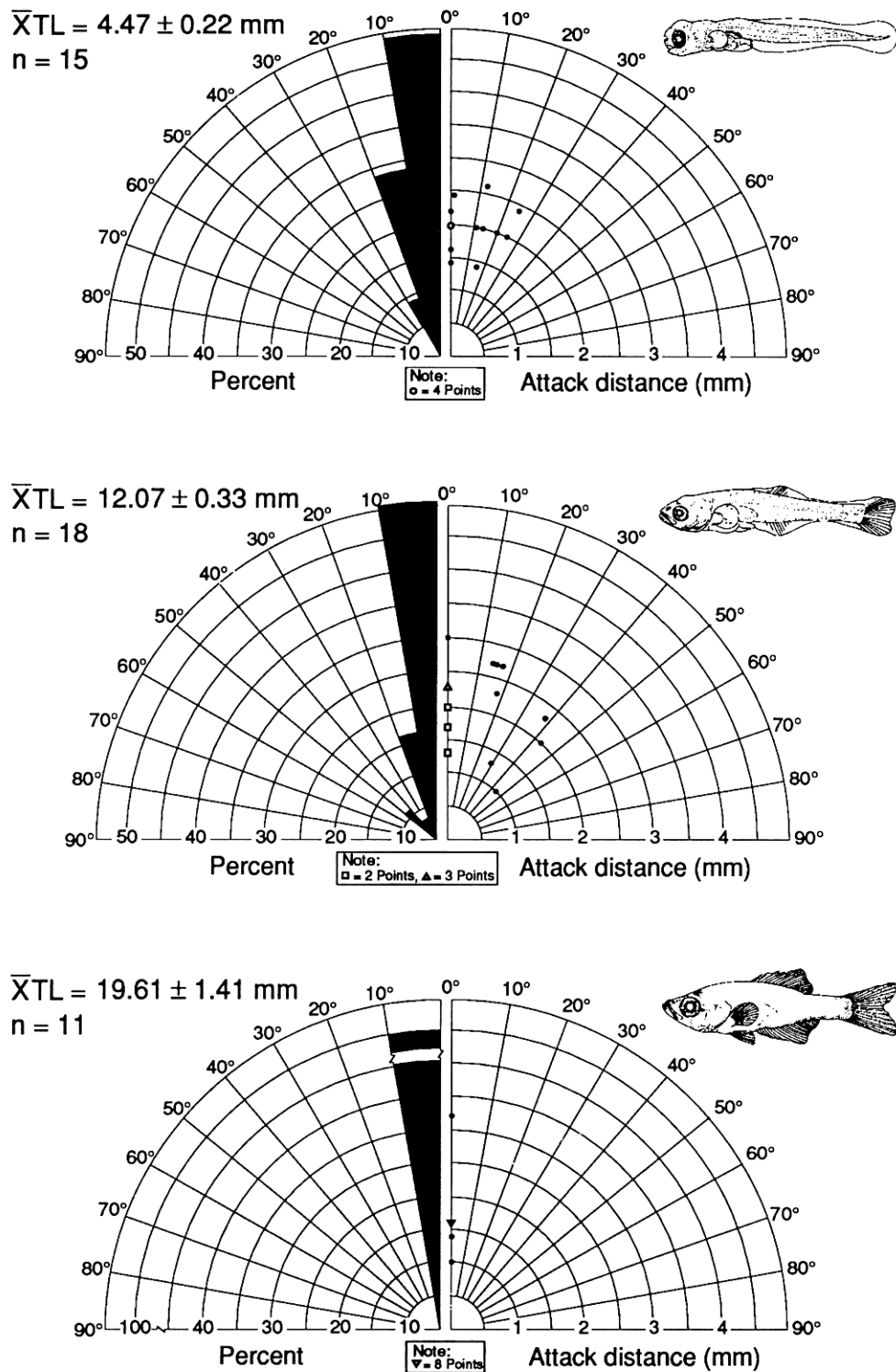


Fig. 7. Size-related changes in attack distances (both left- and right-directed) and angles for white crappie larvae are plotted on the right, and the percent frequency of attacks in each  $10^\circ$  increment of the horizontal visual field are plotted on the left. The points are plotted as if the fish's eyes were positioned in the centre of the polar projection.

*Artemia*. Full S-postures appear to have been employed mostly in attacks on evasive prey such as copepodites. S-posture attacks are no longer exhibited at sizes  $< 20$  mm; feeding strikes are incorporated into more typical swimming movements, as is true for larger juveniles. Meyer (1986, 1987) reported that larvae of the cichlid *Cichlasoma managuense* did not always employ an S-posture in attacks on prey and that the degree to which an S-posture was assumed by these larvae appeared to be modulated by the relative difficulty of capturing prey. The morphological and hydrodynamic aspects of such transitions have recently been addressed in some detail (Drost 1987, Osse 1990).

In general, the size-related changes in the components of the white crappie predation cycle and attack posture that we observed are similar to those reported for other species. For example, swimming speeds, attack speeds, and location and attack distances increase with size in anchovy larvae (Hunter 1972), as is the case for white crappie larvae. Atlantic herring larvae locate prey at angles  $< 70^\circ$  from forward-directed (Rosenthal 1969), as we observed for crappie larvae. Increasing attack success with fish size has been reported for the early life history stages of several species (e.g. Houde & Schekter 1980, Hunter 1980, Blaxter 1986, Meyer 1986, Drost 1987, Meyer 1987). This corresponds to our observation that the proportion of aborted attacks decreased with fish size in white crappie.

Aborted or incomplete attacks, although they are sometimes mentioned (e.g. Braum 1963, Blaxter & Staines 1971, Hunter 1972, Meyer 1986, 1987), have not generally been included in estimates of size-related changes in over-all feeding efficiency. For first-feeding white crappie larvae, a high proportion of all attacks initiated were not followed through. Clearly, aborted attacks must be considered when estimating the feeding efficiency (units: energy, sensu Meyer 1987) of fish larvae.

#### *Search style of white crappie larvae*

In fishes, size-related changes in the components of the predation cycle have not been evaluated from the perspective of search styles. In the following

sections, we describe the prey search pattern employed by white crappie juveniles and address the question of whether, at any given size, white crappie larvae exhibit a similar search pattern.

#### *When does search occur?*

White crappie juveniles search for prey only during the frequent stationary pauses between swimming movements (O'Brien et al. 1986, 1989, 1990). Several lines of evidence support this interpretation.

The duration of stationary pauses in white crappie juveniles is related to the difficulty of locating prey; pause duration is short for large, easily located prey, and longer for small prey that are more difficult to locate (O'Brien et al. 1986, 1989). Further, Ehlinger (1989, 1990) has reported that stationary search time (which he terms 'search-hover' time) in bluegill sunfish, *Lepomis macrochira*, was longer when they were searching for prey in vegetated vs. open-water areas. Assuming that prey are more difficult to locate in structured habitats, Ehlinger's results are consistent with our data for white crappie juveniles feeding on large vs. small prey.

Since visual acuity in young fishes improves rapidly with size (Blaxter 1986, Noakes & Godin 1988, Zaunreiter et al. 1991), the visibility of a given size of prey will increase as a fish grows. The duration of location pauses (SST) in white crappie larvae decreased with fish size, particularly for fish  $> 14$  mm (Fig. 3c). Although the use of *Artemia* in experiments with larger fish may have contributed to this decrease in SST, we consider it preliminary evidence that crappie larvae  $> 14$  mm moderate search time as a function of the difficulty in locating prey.

A characteristic feature that distinguishes 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 its boundary. Crappie juveniles pursue prey throughout the search space (O'Brien et al. 1986, 1989). So do larvae (Fig. 6). The large variation in reaction distances reported for the early life history stages of three cyprinid

species examined by Wanzenböck & Schiemer (1989, their fig. 2) can also be interpreted as evidence that these fish search for prey throughout the search volume.

Pauses between swimming movements may have a function other than search, e.g. time to orient towards 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 level is 1–10%. Further, for every case in which prey were located, orientation towards it did not occur during the stationary pause, but immediately after it, while the fish was engaged in its aiming-attack on prey. These observations are consistent with the saltatory search hypothesis but do not support other interpretations for the function of stationary pauses. We conclude that white crappie larvae search for prey only while stationary.

#### *Relationship between distance moved and search space geometry*

Animals project a scan space while foraging (O'Brien et al. 1989, Tye 1989, O'Brien et al. 1990). The geometry of this space is species-specific and plastic, varying with environmental conditions (background contrast and complexity, light intensity) or prey type (crypsis, size, motility pattern) (Dunbrack & Dill 1984, O'Brien et al. 1986, Evans & O'Brien 1988, Browman et al. 1990). For saltatory searching fishes, which are not searching while moving, the swimming movements between stationary pauses serve to bring the animal into unscanned water. If this is the case, there should be a relationship between the distance traveled and the geometry of the space previously scanned. For example, if after an unsuccessful search an animal moves 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, 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 (O'Brien et al. 1989).

In white crappie juveniles, the geometry of the search space changes with prey type (O'Brien et al. 1986, 1989). Further, the length of swimming moves is directly related to these changes. For example, in juvenile crappie, the maximum location distance for small prey averages 8 cm. The mean move distance for fish searching for small prey is 5.2 cm. Crappie juveniles can locate large daphnid prey at about 20 cm. The mean move distance for fish searching for large daphnids is 9.8 cm. Thus, juveniles make swimming movements that are, on average, about 40% shorter than the maximum distance to which they can detect a prey item. A net energy gain simulation model showed these distances to be optimal (O'Brien et al. 1989).

For crappie larvae, maximum location distance increased with fish size (Fig. 6). Crappie larvae < 12 mm did not efficiently moderate move distance as a function of location distance: for fish in this size range, move distances are longer than location distances (Fig. 5, 6). However, in fish > 12 mm move distances were slightly shorter than location distances, indicating that these fish have begun to modulate their swimming movements in the same manner as juveniles. Thus, after a brief initial period, white crappie larvae appear to modify move distances to minimize redundant search efforts.

The geometry of the search space is also important in determining efficient move distances. When the horizontal dimension of the search space is < 180° (90° on each side of forward-directed), short moves yield a high proportion of unsearched space (see O'Brien et al. 1989). White crappie juveniles exhibit a pie-shaped location space and on average move only 60% of their maximum location distance for any given prey. Because of the geometry of the pie-shape, swimming movements of this distance provide a high proportion of unsearched space (O'Brien et al. 1989).

Maximum search angles in crappie larvae (90° from forward-directed), although smaller than those exhibited by juveniles, are similar to those reported for other fish larvae (Hunter 1972, Wan-

zenböck & Schiemer 1989, Arnold & Holford 1990). However, most locations occur in the first 30°–40° from forward-directed (Fig. 6) and, therefore, for crappie larvae, swimming movements that are relatively close to maximum pursuit distances will yield a high proportion of unsearched space. Mean move distances in fish > 14 mm are indeed only slightly shorter than mean location distances (Fig. 5, 6). We conclude that, at least for larger white crappie larvae, movement patterns are related to search space geometry in a manner similar to that described for juveniles.

#### *Ontogeny of the search style: general considerations*

Virtually all characterizations of search styles in fish larvae imply that they are cruise searchers. 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 & 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 & 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 & Schiemer 1989, Arnold & Holford 1990, reviewed 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.

Our results indicate that at least some crappie larvae are not cruise searchers. Rather, the search pattern that they employ is much like the saltatory search strategy that we have described for juvenile zooplanktivores. This distinction has important ramifications for measuring and interpreting, among other things, predator-prey encounter frequencies, ingestion rates, prey choice and dietary

preferences, and the efficiency of movement patterns associated with foraging (see O'Brien et al. 1989, 1990, Tye 1989). Some specific examples follow.

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. Vlymen's (1977) simulation model of foraging behavior and growth rate in anchovy larvae characterizes their search behavior as occurring in a series of discrete steps that he refers to as 'excursions'. Such a model, which appears to incorporate a stop-and-go search pattern, should produce more realistic estimates of prey encounter. More precise evaluations of encounter rate will allow more accurate estimations of ingestion rates (see MacKenzie et al. 1990).

All else being equal, a saltatory searching fish entering a prey patch should begin to pause more often (although the duration of each pause should decrease), make shorter swimming movements and turns of greater angle. As a result, its mean swimming speed will decrease. Hunter & Thomas (1974) reported that anchovy larvae swam more slowly in patches of *Gymnodinium* than when outside such patches. They also suggested that anchovy larvae responded to the density and distribution of *Gymnodinium* by continual modification of the speed and directional components of their searching behavior. The result of these modifications was an expansion of searching area at low density and a reduction of the area searched at higher food densities. These observations are consistent with the search pattern that we report here and indicate that, when interpreting the results of experiments conducted under conditions of varying prey abundance and distribution, using the fish's average swimming speed to calculate its rate of encounter with prey will yield incorrect estimates.

In summary, we have presented evidence that white crappie larvae search for prey only while stationary and that the search style they employ is similar to that described for juveniles of the spe-

cies. We suggest that careful attention must be paid to size-related changes in the search pattern exhibited by a fish if accurate estimates of feeding rate, growth rate, and other associated variables, are to be obtained. However, we do not advocate use of the saltatory search pattern described herein as an alternate category of prey search that can be used to indiscriminately characterize the search pattern employed by other fishes. We emphasize that accurate evaluations of size-related changes in search patterns require quantifying the components of the search cycle.

### Acknowledgements

This work was supported by NSF grant BSR-8717454 and a University of Kansas Biomedical Research Fund Grant to W.J.O. while 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 J. Showalter for his help in collecting adult white crappie and maintaining larvae, I. Bernard for her help in analyzing the video tapes, and J. Atwater for his assistance with the statistical analysis. Comments and suggestions provided by the following colleagues helped improve the manuscript: W. Bell, J. Brown, C. Chambers, T. Ehlinger, D. Kramer, M. Litvak, G. Maillet, and J. Williams.

### References cited

- Andersson, M. 1981. On optimal predator search. *Theor. Popul. Biol.* 19: 58–86.
- Arnold, G.P. & B.H. Holford. 1990. The reactive perceptive field of the larval plaice (*Pleuronectes platessa* L.): a three-dimensional analysis of visual feeding. *Rapp. P. -v. Comm. Internat. Explor. Mer* 191: 474.
- Arnold, G.P. & P.B.N. Nutall-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 Fishery Commission, Special Publication 82–3. 744 pp.
- Barker, H.R. & B.M. Barker. 1984. Multivariate analysis of variance (MANOVA). A practical guide to its use in scientific decision making. The University of Alabama Press, Tuscaloosa. 160 pp.
- Bell, W.J. 1990. Searching behaviour. The behavioural ecology of finding resources. Chapman & Hall, New York. 400 pp.
- Blaxter, J.H.S. 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Trans. Amer. Fish. Soc.* 115: 98–114.
- Blaxter, J.H.S. & M.E. Staines. 1971. Food searching potential in marine fish larvae. pp. 467–485. *In*: D.J. Crisp (ed.) Fourth European Marine Biology Symposium, Cambridge University Press, Cambridge.
- Braum, E. 1963. Die ersten Beutefanghandlungen junger Blaufelchen (*Coregonus wartmanni* Bloch) und Hechte (*Esox lucius* L.). *Z. Tierpsychol.* 20: 257–266.
- Braum, E. 1964. The survival of fish larvae with reference to their feeding behaviour and the food supply. pp. 113–131. *In*: S.D. Gerking (ed.) The Biological Basis of Freshwater Fish Production, Blackwell Scientific, Oxford.
- Browman, H.I. 1989. Behavioral ecology of foraging in a zooplanktivorous fish, *Pomoxis annularis*, and a predaceous invertebrate, *Leptodora kindti*: ontogenetic and neuroethological perspectives. Ph.D. Dissertation, The University of Kansas, Lawrence. 169 pp.
- Browman, H.I., W.C. Gordon, B.I. Evans & W.J. O'Brien. 1990. Correlation between histological and behavioral measures of visual acuity in a zooplanktivorous fish, the white crappie (*Pomoxis annularis*). *Brain, Behav. Evol.* 35: 85–97.
- Browman, H.I., S. Kruse & W.J. O'Brien. 1989. Foraging behavior of the predaceous cladoceran, *Leptodora kindti*, and escape responses of their prey. *J. Plank. Res.* 11: 1075–1088.
- Brown, J.A. & P.W. Colgan. 1984. The ontogeny of feeding behaviour in four species of centrarchid fish. *Behav. Process* 9: 395–411.
- Brown, J.A. & P.W. Colgan. 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.
- Dunbrack, R.L. & L.M. Dill. 1984. Three dimensional prey reaction field of the juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 41: 1176–1182.
- Edgerton, H.E. 1977. Silhouette photography of small active subjects. *J. Microsc.* 110: 79–81.
- Ehlinger, T.J. 1989. Learning and individual variation in bluegill foraging: habitat-specific techniques. *Anim. Behav.* 38: 643–658.
- Ehlinger, T.J. 1990. Habitat choice and phenotypic-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. *Ecology* 71: 886–896.
- Ehlinger, T.J. & D.S. Wilson. 1988. Complex foraging poly-

- morphism in bluegill sunfish. *Proc. Natl. Acad. Sci. USA* 85: 1878–1882.
- Evans, B.I. & 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.
- Heidinger, R.C., B. Tetzlaff & J. Stoeckel. 1985. Evidence of two feeding subpopulations of white crappie (*Pomoxis annularis*) in Rend Lake, Illinois. *Jour. Freshw. Ecol.* 3: 133–143.
- Houde, E.D. & R.C. Schekter. 1980. Feeding by marine fish larvae: developmental and functional responses. *Env. Biol. Fish.* 5: 315–334.
- Huey, R.B. & E.R. Pianka. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991–999.
- Hunter, J.R. 1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. *U.S. Fish. Bull.* 70: 821–838.
- Hunter, J.R. 1977. Behavior and survival of northern anchovy, *Engraulis mordax*, larvae. *Calif. Coop. Oceanic Fisher. Invest. Rep.* 19: 138–146.
- Hunter, J.R. 1980. The feeding behavior and ecology of marine fish larvae. pp. 287–330. *In*: J.E. Bardach, J.J. Magnuson, R.C. May & J.M. Reinhart (ed.) *Fish Behavior and Its Use in the Capture and Culture of Fishes*, ICLARM Conf. Proceed. 5, Manila.
- Hunter, J.R. & G.L. Thomas. 1974. Effect of prey distribution and density of the searching and feeding behaviour of larval anchovy *Engraulis mordax* Girard. pp. 559–574. *In*: J.H.S. Blaxter (ed.) *The Early Life History of Fish*, Springer-Verlag, New York.
- 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.
- Lachenbruch, P.A. 1975. Discriminant analysis. Hafner Press, New York. 227 pp.
- MacKenzie, B.R., W.C. Leggett & R.H. Peters. 1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? *Mar. Ecol. Prog. Ser.* 67: 209–225.
- Marcy, D.E. 1954. The food and growth of the white crappie, *Pomoxis annularis*, in Pymatuning lake, Pennsylvania and Ohio. *Copeia* 1954: 236–239.
- Mathur, D. & T.W. Robbins. 1971. Food habits and feeding chronology of the young white crappie, *Pomoxis annularis* Rafinesque in Conowingo reservoir. *Trans. Amer. Fish. Soc.* 100: 307–311.
- McLaughlin, R.L. 1989. Search modes of birds and lizards: evidence for alternative movement patterns. *Amer. Nat.* 133: 654–670.
- Meyer, A. 1986. Changes in behavior with increasing experience with a novel prey in fry of the Central American cichlid, *Cichlasoma managuense* (Teleostei: Cichlidae). *Behaviour* 98: 145–167.
- Meyer, A. 1987. First feeding success with two types of prey by the Central American cichlid fish, *Cichlasoma managuense* (Pisces, Cichlidae): morphology versus behavior. *Env. Biol. Fish.* 18: 127–134.
- Noakes, D.L.G. & J.-G.J. Godin. 1988. Ontogeny of behavior and concurrent developmental changes in sensory systems in teleost fishes. pp. 345–395. *In*: W.S. Hoar & D.J. Randall (ed.) *Fish Physiology*, Volume 11B, Viviparity and Post Hatching Juveniles, Academic Press, New York.
- O'Brien, W.J., H.I. Browman & B.I. Evans. 1990. Search strategies in foraging animals. *Amer. Sci.* 78: 152–160.
- O'Brien, W.J., B.I. Evans & 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 & G. Howick. 1986. A new view of the predation cycle in a planktivorous fish. *Can. J. Fish. Aquat. Sci.* 43: 1894–1899.
- O'Brien, W.J., B. Loveless & D. Wright. 1984. Feeding ecology of young white crappie in a Kansas reservoir. *N. Amer. J. Fisher. Manag.* 4: 341–349.
- Osse, J.W.M. 1990. Form changes in fish larvae in relation to changing demands of function. *Nether. J. Zool.* 40: 362–385.
- Rosenthal, H. 1969. Investigations regarding the prey catching behavior in larvae of the herring (*Clupea harengus*). *Mar. Biol.* 3: 208–221.
- Rosenthal, H. & G. Hempel. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.). pp. 344–364. *In*: J.H. Steele (ed.) *Marine Food Chains*, Oliver & Boyd, Edinburgh.
- Schoener, T.W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. System* 2: 369–404.
- Scott, W.B. & E.J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin No 184, Ottawa. 966 pp.
- Statistical package for the social sciences. 1987. SPSS/PC + Advanced Statistics Guide v2.0, McGraw-Hill Book Co., New York. 360 pp.
- 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.
- Vlymen, W.J. 1977. A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution, and larval behavior. *Env. Biol. Fish.* 2: 211–233.
- Wanzenböck, J. 1992. Ontogeny of prey attack behaviour in larvae and juveniles of three European cyprinids. *Env. Biol. Fish.* 33: 23–32.
- Wanzenböck, J. & F. Schiemer. 1989. Prey detection in cyprinids during early development. *Can. J. Fish. Aquat. Sci.* 46: 995–1001.
- Zaunreiter, M., H. Junger & K. Kotrschal. 1991. Retinal morphology of cyprinid fishes: a quantitative histological study of ontogenetic changes and interspecific variation. *Vision. Res.* 31: 383–394.