

Ontogenetic variations in the foraging behaviour of the cyprinid fish *Vimba elongata*: size- and age-specific responses to novel prey

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Summary

Results from field studies demonstrate that *Vimba elongata* (Cyprinidae) from Mondsee undergo marked shifts in vertical habitat use and diet selection during early as well as during late ontogenetic stages. To investigate whether such shifts may be induced by age-specific sensitive phases or by size-related factors, laboratory reared *V. elongata* belonging to four different age-classes (two of them with overlapping body size) were exposed to red chironomid larvae offered as novel prey at the bottom of glass tanks. Significant differences among the four age-classes were found in the latencies of first snap at the novel prey as well as in the fish's prey capture and snapping performance. Age-classes 2 and 3 showed short latencies indicating a phase of increased sensitivity to bottom dwelling prey. Age-classes 1 and 2 showed low capture rates as a consequence of their small body sizes. Age-class 4 responded to the novel foraging condition slowly and conservatively. Fish of age-class 3 had much higher capture and total snapping rates than all others. This age-class also showed some initial problems in discriminating the prey from prey-like dummies, but subsequently learned to reduce the proportion of snaps at these optic distractors. These results and the data from earlier experimental investigations on the foraging behaviour of six cyprinid species lead to the conception of prey search as a process of attentional priming. From the present study follows that age and size may provide differential contributions to ontogenetic variations in *V. elongata* foraging behaviour.

Zusammenfassung

Bei Freilanduntersuchungen an *Vimba elongata* aus der Familie der Karpfenfische (Cyprinidae) im Mondsee wurden ontogenetische Verschiebungen in Habitatnutzung und Nahrungswahl festgestellt, welche sowohl während früher als auch während späterer Lebensstadien ablaufen. Um zu untersuchen, ob diese ontogenetischen Verschiebungen durch altersspezifische, prägungsähnliche Vorgänge oder durch größenabhängige Faktoren induziert werden, wurden laboraufgezoogene *V. elongata* aus vier verschiedenen Altersklassen (zwei davon mit überlappender Körpergröße) in Verhaltensexperimenten mit roten Zuckmückenlarven als neuer Bodenbeute konfrontiert. Zwischen den vier Altersklassen zeigten sich deutliche Unterschiede in den Latenzen der ersten Attacke auf diese neue Beute sowie in der Beutefangleistung und der Schnappaktivität. Die Altersklassen 2 und 3 zeigten sehr kurze Latenzen, welche auf eine altersspezifische Phase mit erhöhter Sensibilität gegenüber Bo-

denbeute hinweisen. Die Altersklassen 1 und 2 zeigten geringe Beutefangraten als Konsequenz ihrer relativ kleinen Körpergröße. *V. elongata* von Altersklasse 4 reagierten auf die neuen Ernährungsbedingungen eher langsam und konservativ. Die Altersklasse 3 zeigte wesentlich höhere Beutefang- und Schnappraten als alle anderen getesteten Fische. Diese Altersklasse zeigte anfängliche Probleme in der Unterscheidung zwischen der neuen Beute und beuteähnlichen Plastikattrappen, lernte aber im weiteren Verlauf der Experimente den Anteil der auf diese visuellen Störobjekte gerichteten Schnapper zu reduzieren. Diese Ergebnisse und die Daten aus experimentellen Arbeiten zur Öko-Ethologie des Nahrungserwerbs von insgesamt sechs Karpfenfischarten führen zur Konzeption der Beutesuche als Prozeß der Aufmerksamkeitseinstellung. Aus der vorliegenden Untersuchung kann geschlossen werden, daß Alter und Körpergröße unterschiedliche Einflüsse auf ontogenetische Veränderungen im Nahrungserwerbsverhalten von *V. elongata* ausüben.

Introduction

Age and size are important variables that induce fishes to change their foraging behaviour during ontogeny. With increasing size, sensory and prey manipulation organs become larger and more efficient leading to improvements in prey search and handling abilities. With increasing age, more and more learned information becomes available.

In young fishes, age and size act primarily as constraints restricting the foraging success to small and easily obtainable food types (NICOL, 1989, MILLER et al., 1992, WALTON et al., 1992), and delaying or reinforcing learning of novel food types during sensitive phases (GODIN, 1978, MEYER, 1988).

During later development, food and foraging mode selection may be modified by earlier experience with proper food types or habitat features (COLGAN et al., 1986, MEYER, 1986, NOLTIE & JOHANSEN, 1986). Older and larger fish often select larger prey, use more profitable search and handling techniques, and forage in different microhabitats than younger ones (WERNER, 1974, GROSSMAN et al., 1980, LIEM, 1984, WERNER & GILLIAM, 1984, UIBLEIN & WINKLER, 1987, UIBLEIN, 1991).

Until now, most experimental work on the effects of age and size on fish foraging behaviour has been devoted to the study of fish larvae and small juveniles. However, recent field data on food searching activities and diet selection in some marine and freshwater species indicate that fishes may alter their foraging behaviour significantly throughout their lifetimes (UIBLEIN & WINKLER, 1987, UIBLEIN, 1991, EGGOLD & MOTTA, 1992, SANDLUND et al., 1992).

Vimba elongata are cyprinid fish which live in prealpine lakes of Austria and Bavaria (UIBLEIN & WINKLER, 1994). During the first year of life this species shifts from a surface-dwelling to a benthic lifestyle (UIBLEIN et al., 1987). In the following two years this species consumes benthic and epibenthic crustaceans and insect larvae almost exclusively. Age-classes older than three years feed frequently on mollusks, benthic

crustaceans, and insect larvae. During summer however, when zooplankton abundance increases, older *V. elongata* consume large quantities of zooplankton (UIBLEIN & WINKLER, 1987).

In the current experimental study, laboratory-reared *V. elongata* belonging to four different age-classes (two of them with overlapping body size) were exposed to chironomids offered as novel bottom prey in foraging experiments. The following predictions were tested: (1) *V. elongata* undergo age-specific shifts in foraging behaviour which are at least partly independent of body size. (2) Such ontogenetic shifts happen during early as well as during late developmental stages.

Material and Methods

Sixteen specimens of *Vimba elongata* (Val.), belonging to four different age-classes (Table 1) were tested individually. All fish originated from the Mondsee (a mesotrophic, temperate lake in Upper Austria) and had been hatched and reared under controlled conditions and fed exclusively with zooplankton until the start of the experiments.

Age-class	N	Age (in months)	Mean (range) of SL (in mm)
1	3	7	47.3 (47– 48)
2	3	19	48.0 (45– 51)
3	5	25	69.6 (66– 71)
4	5	50	101.0 (96–109)

Table 1. Number of individuals tested, age, and mean standard length (with ranges in parentheses) in the four age-classes of *Vimba elongata*.

Tabelle 1. Anzahl von untersuchten Individuen, Alter und durchschnittliche Standardlänge (mit Reichweiten in Klammern) der vier Altersklassen von *V. elongata*.

The four age-classes differed significantly among each other in size with the exception of age-classes 1 and 2 (one-way ANOVA, $F_{(3,12)} = 216$, $p < 0.0001$; SCHEFFE multiple range test; Table 1). The size overlap was produced solely by rearing age-class 1 at a lower density than age-class 2. All four age-classes were fed a rich supply of zooplankton three times daily to keep competition for food at a minimum.

For the experiments, the fish were transferred into glass tanks (20 x 30 cm² bottom) that had been positioned above a black cardboard background and filled with 8 l of filtered water from the Mondsee. Temperature was kept constant at 19 ± 1 °C. Light was provided at 600 ± 50 Lux for intervals of 12 h, in alternation with 12 h of total darkness. Experimental sessions were carried out at 24 h intervals between 13:00 and 15:00 h. The experimental tanks were surrounded by white styrofoam-walls with a small window for observations.

With each single fish successive experimental sessions were carried out with 10 red living chironomid larvae (*Chironomus* sp., 5–6 mm length) offered as novel, benthic prey. While the experimental conditions were prepared, the fish were enclosed behind a partition for about 5 min.

Then the tank was cleaned and the prey introduced. The experiments started when the partition was removed and the fish had free access to the prey. In addition to the prey, ten red chironomid-like plastic dummies were distributed on the bottom of the tanks. The purpose of these dummies was to provide the experimental fish with optic distractors to examine their visual search capabilities.

Latency was measured as the total time interval of prey exposure until the first snap at prey. In each experimental session, the fish were confronted with the prey for maximally 15 min. In eight individuals, no snaps at prey occurred during the first presentation of the novel prey. In these cases, the respective sessions were suspended and continued after 24 h. For five individuals, which still showed no response during the 15 min of this second presentation, the same procedure was repeated until they also started to snap at the prey. After four repetitions, all fishes had started to snap at the prey. This experimental treatment allowed prey exposure time to be increased without any observable disturbance of fish behavioural performance (see also UIBLEIN et al., 1992).

The numbers of snaps at prey items or dummies ("directed snaps") and snaps at inconspicuous particles ("undirected snaps") were recorded for a total time span of five minutes beginning with the first snap directed at prey. The frequency of snaps resulting in prey ingestion ("captures"), the frequency of unsuccessful snaps at prey, and the frequency of snaps at dummies were also recorded. In all experimental sessions, the highest foraging rates occurred within the first 40 seconds and hence the data analysis was restricted to this time interval.

A two-way ANOVA for repeated measures was employed to examine latencies and snap rates (the number of snaps per 40 seconds) for significant differences among age-classes and experimental sessions. DUNCAN's range test was used for a posteriori multiple comparisons among age-classes (significance level $p < 0.05$).

For statistical comparisons of percent values with a G-test, data of individual fish had first to be pooled (SOKAL & ROHLF, 1981). Pooling of the data was justified as no individual differences were detected within any single session (G-test, $p > 0.05$; see also UIBLEIN, 1992 a).

Results

Latencies showed a significant decline among the three sessions, from mean 3010 to 107.3 s in age-class 1, from 390.7 to 66.3 s in age-class 2, from 593.4 to 39.8 s in age-class 3, and from 1854.8 to 215.8 s in age-class 4 ($F_{(2,24)} = 26.44$, $p < 0.0001$; Fig. 1). A comparison of the latencies among the four age-classes revealed a clear separation in the first experimental session between the three individuals belonging to age-class 1 and the eight individuals belonging to age classes 2 and 3 (Table 2). Furthermore, significant differences among the four age-classes were found with respect to the complete data set ($F_{(3,12)} = 6.77$, $p < 0.01$). DUNCAN's range test separated the latency-data into two groups, one consisting of age-classes 1 and 4, and the other of age-classes 2 and 3. The

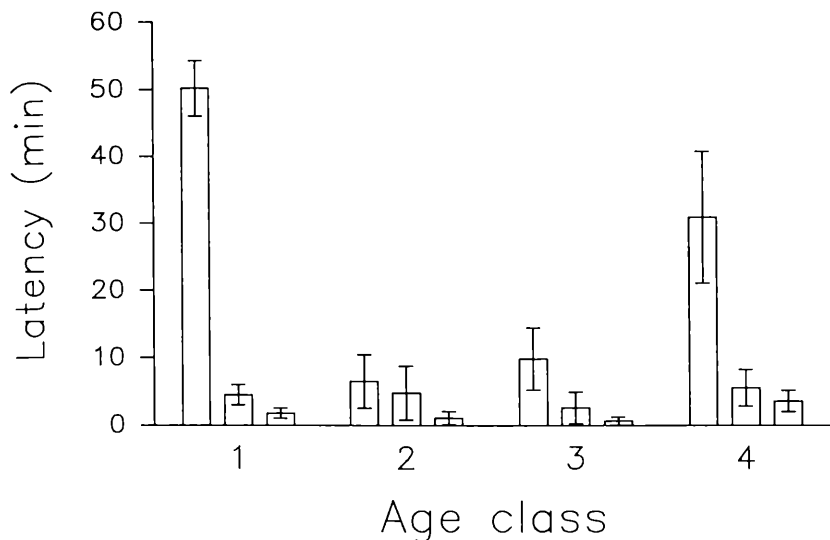


Fig. 1. Mean latency of first snap at prey in four age-classes of *Vimba elongata* in three successive sessions (with SE of the mean).

Abb. 1. Durchschnittliche Latenz der ersten Attacke auf Beute bei vier Altersklassen von *V. elongata* während drei aufeinanderfolgender Sitzungen (mit Standardfehler des Mittelwertes).

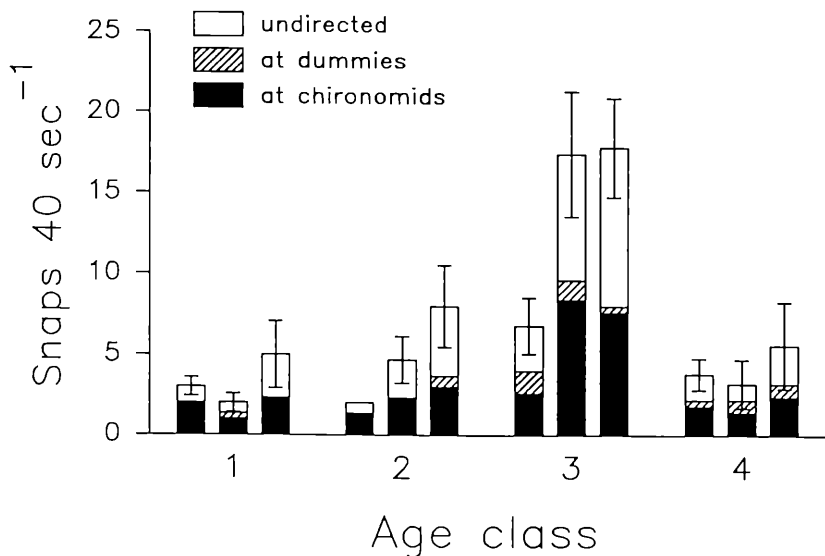


Fig. 2. Mean frequency of snaps per 40 s in four age-classes of *Vimba elongata* in three successive sessions (with SE of the mean).

Abb. 2. Durchschnittliche Frequenz von Schnappern pro 40 Sekunden bei vier Altersklassen von *V. elongata* während drei aufeinanderfolgender Sitzungen (mit Standardfehler des Mittelwertes).

Age-class	Session 1	Session 2	Session 3
1	3010.0 (2570–3423)	271.3 (143–443)	107.3 (30–185)
2	390.7 (11–840)	287.3 (8–766)	66.3 (4–181)
3	593.4 (82–1592)	157.2 (5–719)	39.8 (3–185)
4	1854.8 (661–3737)	332.8 (64–900)	215.8 (22–496)

Table 2. Mean latency (in s; with ranges in parentheses) of first snap at novel prey in four age-classes of *Vimba elongata* during three successive experimental sessions (for further informations see Table 1).

Tabelle 2. Durchschnittliche Latenz (in Sekunden; mit Reichweiten in Klammern) der ersten Attacke auf neue Beute bei vier Altersklassen von *V. elongata* während drei aufeinanderfolgender experimenteller Sitzungen (für weitere Informationen siehe Tabelle 1).

interactions between the two factors (session and age-class) were significant ($F_{(6,24)} = 5.15$, $p < 0.01$).

The number of total snaps increased significantly among sessions from mean 3.0 to 5.0 snaps per 40 s in age-class 1, from 2.0 to 8.0 snaps in age-class 2, from 6.8 to 17.8 snaps in age-class 3, and from 3.8 to 5.6 snaps in age-class 4 ($F_{(2,24)} = 10.1$, $p < 0.001$, Fig. 2). Significant variations also occurred among the four age-classes ($F_{(3,12)} = 7.32$, $p < 0.005$) with main differences between age-class 3 and all others. The interactions between the two factors were also significant ($F_{(6,24)} = 3.08$, $p < 0.025$).

46.8 % of the total 348 snaps observed were undirected, independent of either experience with the novel prey or age-class (G-test, $p > 0.05$).

15.1 % of the total 185 directed snaps recorded were directed at dummies. Age-class 3 showed a significant decrease in the relative frequency of snaps at dummies from 35 % in the first session to 5 % in the third session (G-test, $\chi^2 = 8.63$, $p < 0.025$). For this category, no other significant variations were found among age-classes or sessions in all combinations ($p > 0.05$).

Of the 157 snaps directed at prey items, only 3.8 % failed to result in prey ingestion. Similar to the number of total snaps, the rate of successful captures increased significantly among sessions, from mean 2.0 to 2.3 captures per 40 s in age-class 1, from 1.3 to 3 captures in age-class 2, from 2.6 to 7.6 captures in age-class 3, and from 1.4 to 2.2 captures in age-class 4 ($F_{(2,24)} = 18.22$, $p < 0.0001$; Fig. 2). Among age-classes significant variations were also detected ($F_{(3,12)} = 13.36$, $p < 0.001$), with main differences between age-class 3 and all others. In addition, the two factors interacted significantly ($F_{(6,24)} = 7.77$, $p < 0.001$).

Discussion

Differences in latencies frequently occur when attention is focused at certain locations of the surrounding space (THINUS-BLANC, 1988, WILLIAMS et al., 1990). Fishes often prefer to search for food at distinct vertical positions (LARSON, 1976, UIBLEIN, 1988). If profitable prey emerges at a previously unfocused, higher or lower position, attention has to be shifted to that novel location what costs time.

In the Mondsee, *V. elongata* show a marked shift in vertical food search from the surface to the bottom zone during their first year of life. Then they feed on benthic and epibenthic prey exclusively until about three years old (UIBLEIN et al., 1987, UIBLEIN & WINKLER, 1987). All fish used in the present study had been reared in the laboratory under identical conditions. Nevertheless, when exposed to the novel bottom prey for the first time, *V. elongata* belonging to age-classes 2 and 3 had shorter latencies of first snapping than age-class 1 (Table 2). Age-classes 1 and 2 overlapped in body size, while age-class 3 was clearly larger sized (Table 1). These results indicate that one-year old *V. elongata* enter an age-specific and probably size-independent phase of increased sensitivity to bottom prey which is accompanied by a shift in vertical food search position.

From age-class 4 onwards, the sensitivity to bottom prey may weaken and vertical food search is shifted towards the surface, from where the zooplankton food had been introduced during the entire rearing period. In tall holding tanks of the laboratory four-years old *V. elongata* rose to the surface and snapped there at high frequencies even when food introduction was only simulated (personal observations). In the Mondsee, *V. elongata* older than four years still feed on benthic prey, but switch to zooplankton feeding during summer (UIBLEIN & WINKLER, 1987). Instead of orienting vertical food search towards novel prey locations, older fish may increasingly use prey occurrence informations experienced during earlier periods of their lives.

All age-classes showed similar rates of undirected snaps, a search behaviour used by *V. elongata* to explore the environment beyond visual prey detectability (UIBLEIN, 1992 a). A similar search mode has been found in several other fish species and termed sampling (GODIN, 1986, UIBLEIN, 1992 b) or probing (SIBBING et al., 1986).

The chironomids offered as experimental prey had relative lengths of more than 10 % of fish length in age-classes 1 and 2 and may have affected the prey capture rate of these small sized fish significantly. When gammarids with relative lengths of about 3 % were offered as novel bottom prey to one-year old *V. elongata*, the fish increased total snap and capture rates clearly faster (UIBLEIN, 1988). Large relative prey size limits the prey capture activity in many fishes by increasing handling times and reducing attack rates (MILLER et al., 1992, WALTON et al., 1992).

The low total number of snaps and captures in age-class 4 cannot be attributed to a large relative prey size, because the smaller age-class 3 showed significantly higher foraging rates with the same prey type. In this case, the results indicate rather a loss of quickness to adjust behaviourally to novel prey types in older fish (see also MEYER, 1986, OSENBERG et al., 1992).

V. elongata of age-class 3 detected novel bottom prey faster and increased total snaps and prey captures to a much higher extent than all other age-classes. This age-class showed initial problems of visual discrimination, but clearly reduced the proportion of snaps at dummies

between the first and the third session. In this case, learning of previously detected, novel prey proceeded in two aspects: (1) An increase in total search rate (GENDRON & STADDON, 1983). (2) An improvement of visual discrimination (BOND & RILEY, 1991). Animals which search faster encounter more prey items but also more optic distractors that reduce the time available to choose the correct targets. Search efficiency can be further increased by priming attention to those specific prey characteristics that best distinguish the prey from their immediate surroundings (REID & SHETTLEWORTH, 1992).

The current study and the results of earlier experimental investigations on the foraging behaviour of *V. elongata* and five other cyprinid species (UIBLEIN, 1988, UIBLEIN, 1992 a, 1992 b, UIBLEIN et al., 1992, UIBLEIN, 1994) suggest that these fishes undergo various stages of attentional priming during novel foraging situations. After previous detection of a novel prey type, vertical food search position is altered and total snapping activity is increased with a distinct proportion of snaps aimed at visual prey cues. Individuals with a quick activity increase are in particular faced with initial discrimination problems and develop a more accurate representation of prey visual characteristics during further encounters.

As reported earlier, cyprinids including *V. elongata* show species-specific and prey-specific differences in the behavioural response to novel prey (UIBLEIN, 1992 b, UIBLEIN et al., 1992). The current study suggests that *V. elongata* undergo age- and size-specific variations, too. Accordingly, age and size may provide differential contributions to ontogenetic variations in the foraging behaviour of *V. elongata* with body size affecting prey handling performance and age acting as a constraint upon spatial food search and learning of novel prey.

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