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Reaction field, capture field, and search volume of 0+ nase (*Chondrostoma nasus*): effects of body size and water velocity

L. Flore, W. Reckendorfer, and H. Keckeis

Abstract: The reaction field, capture field, and search volume of four size-classes of 0+ nase (*Chondrostoma nasus*) were investigated at two water velocity regimes using flow-tank experiments. Reactive and capture distances, measured in three dimensions, increased linearly with fish size and were larger in flowing water than in calm water. The 0+ nase reacted almost exclusively to prey that were situated in their forward-directed hemisphere. In flowing water, 0+ nase systematically drifted and (or) swam downstream with the current in pursuit of prey that had drifted past their stations. Captures thus occurred in their backward-directed hemisphere. Based on the fish's swimming speed and its reaction field, we propose a modified method for estimating search volume of 0+ nase and other rheophilic cyprinid species with a similar feeding mode. Search volume also increased linearly with fish size and was larger in flowing water than in calm water. We argue why the foraging mode of 0+ nase in flowing water is the effect of a constraint imposed by water current rather than the result of an economic strategy.

Résumé : On a étudié le champ de réaction, le champ de capture et le volume de recherche de quatre classes de taille de nase commun (*Chondrostoma nasus*) d'âge 0+ à deux régimes de vitesse de courant dans le cadre d'expériences réalisées en bassin. Les distances de réaction et de capture, mesurées en trois dimensions, augmentaient linéairement avec la taille des poissons et étaient plus grandes en eau vive qu'en eau calme. Les nases réagissaient presque exclusivement aux proies qui se trouvaient devant eux, soit dans l'hémisphère antérieur. En eau vives, les nases dérivaient et (ou) nageaient systématiquement dans le sens du courant à la poursuite des proies qui avaient dérivé derrière leur position. Les captures se produisaient alors dans l'hémisphère postérieur des nases. Sur la base de la vitesse de nage et du champ de réaction des nases, nous proposons une méthode modifiée pour estimer le volume de recherche des nases d'âge 0+ et d'autres cyprinidés rhéophiles se nourrissant de façon similaire. Le volume de recherche augmentait aussi linéairement avec la taille des poissons et était plus gros en eau vive qu'en eau calme. Nous expliquons pourquoi le mode d'alimentation des nases d'âge 0+ en eau vive est fonction de la contrainte imposée par le courant plutôt que le résultat d'une stratégie énergétique.

[Traduit par la Rédaction]

Introduction

Visually mediated foraging has been well studied in planktivorous freshwater fish (O'Brien et al. 1989; Aksnes and Utne 1997), and it has been shown that basic components determining the foraging efficiency — the search for food, the reaction to the prey, and its capture — change during ontogenetic development. Improvement in the fish's visual resolution allows the fish to search a larger volume of water for prey at any one time (Hairston et al. 1982; Walton et al. 1994). Besides the improvement in the visual system, the development of the swimming muscles and efficient propulsive movements permits the fish to enlarge the capture field (Nyberg 1971; Kaufmann 1990).

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Within the environmental parameters, water velocity has a major bearing on the reaction field and capture field of stream-dwelling fish. It has been demonstrated that reactive distance and capture distance of salmonids decreased at high water velocity (Godin and Rangeley 1989; O'Brien and Showalter 1993). Godin and Rangeley (1989) showed that the changes in capture distance with water velocity resulted from decision making by the forager in response to increased costs of locomotion.

The components of the reactive field have been used to elaborate predictive models of search volume and thus of prey encounter probability (O'Brien and Evans 1992; Eiane et al. 1997). In order to provide an unbiased estimation of the search volume, the reaction fields should be examined in three dimensions (Luecke and O'Brien 1981). Dunbrack and Dill (1984) stressed the importance of assessing the shape of the reaction fields, which will depend on the foraging mode. For saltatory fish that search briefly while stationary in calm water (e.g., Arctic grayling (*Thymallus arcticus*)), the search volume developed by O'Brien et al. (1989) and later used by Walton et al. (1994) was presented as a pieshaped wedge of the visual field that is located rostal to the fish's snout. Cruising fish move through the water column and search for food without pausing and may therefore perceive their prey somewhat differently, e.g., due to an alteration in their apparent motion (Dunbrack and Dill 1984). For such predators, the search volume is described in the literature as somewhat cylindrical and whose longitudinal axis is the fish's trajectory (Eggers 1977; Confer et al. 1978; Wanzenböck and Schiemer 1989). All of these models do not consider the blind region in front of the fish (Luecke and O'Brien 1981; Wanzenböck and Schiemer 1989; Walton et al. 1994), leading to an overestimation of their search volume.

To date, there is still an evident lack of information concerning the feeding ecology of rheophilic cyprinids. The nase (*Chondrostoma nasus*), was once very common in numerous European rivers and is now regarded as a target endangered rheophilic species (Keckeis et al. 1997). The young stages of the nase are distributed along the river margins and are thus exposed to different water velocity regimes. They occur in calm water habitats as well as in flowing water environments. Up to a body length of 40–50 mm, they feed on zooplankton and drifting invertebrates (Reckendorfer et al. 1999). It is not yet known which strategy is used by the nase while searching for food, reacting to the prey, and capturing it. Should they be considered as saltatory or cruising fish in calm water? Do they behave as stream-dwelling fish in flowing water?

In the present work, we qualify the feeding behaviour of the young nase under two water velocity regimes. We quantify the components of their reaction and capture fields in three dimensions as well as their changes with fish size and water velocity. We propose a modified version of the cylindrical model (Eggers 1977; Confer et al. 1978; Wanzenböck and Schiemer 1989) to calculate the search volume of 0+ nase and other reophilic cyprinids with a similar searching mode. The modification considers the blind region in front of the fish and allows the determination of the shape of the reaction and capture fields on a sound statistical basis.

Materials and methods

Rearing conditions

Fish larvae were obtained by artificial fertilization from adults caught in the Fischa River, a tributary of the Danube River (Keckeis et al. 1996). Fish stocks were kept in circular pools (60 L) with constant water flow at 16°C. They were fed ad libitum with *Artemia salina* nauplii, *Daphnia magna*, and food pellets. Larval and juvenile stages of nase were defined according to Penáz (1974). Four size-classes (millimetres) were studied (means with total length (TL) ±SD and development stage in parentheses): 20 (19.6 ± 0.78, fifth and sixth larval stages), 25 (24.5 ± 0.68, first juvenile stage), 35 (35.49 ± 0.59), and 45 (45.51 ± 0.82, late juvenile stage).

Experimental design

Experiments were conducted in a recirculating flume (300 × 50 × 50 cm). From pilot observations, a volume of 7500 cm^3 for 20–25 mm TL, 15 000 cm^3 for 35 mm TL, and 21 000 cm^3 for 45 mm TL was found to be sufficient to ensure freedom of movement. Water temperature was maintained at 16°C and water depth at 10 cm. Individuals were starved 24 h before the beginning of experiments. Pilot trials showed that single fish had disturbed feeding behaviour. Groups of eight individuals were thus used. Experiments were replicated six times using different groups of fish. The individuals were allowed to adjust at least 0.5 h before the beginning of the tests. *Daphnia magna* was cultured in the laboratory and used as prey in the experiments. One distinct size-class (0.99 ± 0.08 mm) accessible to fish was produced by sequential sieving. Drifting invertebrates, including Cladocera, represent the main food component (>70%) found in the gut of 0+ nase (Reckendorfer et al. 1999). Prey were introduced into the channel via a funnel and tube delivery system. The prey were equally distributed in the water column. In order to consider the role of the entire foraging field, our measurements were performed in three dimensions, as in, for example, Luecke and O'Brien (1981) and Dunbrack and Dill (1984). This was achieved by using two synchronized cameras. The recordings were analyzed with image analysis software (Optimas) (Flore and Keckeis 1998). A detailed description of the technical installation, video equipment, and experimental design is given in Flore and Keckeis (1998).

Three-dimensional analyses

The paired video records were used to obtain the coordinates (*x,y,z*) of (*i*) the fish's snout position just prior to attack initiation, (*ii*) the position of the prey just prior to the attack initiation, and (*iii*) the prey position at the point of capture.

Reaction and capture field map

The nase reaction field and capture field were mapped in three planes: transverse (*YZ*, through the eyes), horizontal (*XY*, along the midbody line), and sagittal (*XZ*) (Fig. 1*a*).

For each plane, the projections of the prey positions at reaction and capture, respectively, were plotted relative to the fish's snout position (i.e., the fish's snout position at reaction (*x,y,z*) was set to 0,0,0). The points obtained in the right hemisphere were reflected to the left hemisphere. Only 4.7% of the capture reactions occurred below the fish's horizontal plane. They were thus not included in the map. The following parameters were measured or calculated.

Vertical position of the fish in the water column: percentage of time spent in each of three defined vertical layers of 3.3 cm height (upper, middle, lower).

Cruising speed (CSp): the fish's swimming speed when searching for prey in calm water.

Reaction angle in the three planes (β): the angle between the body axis prior to the attack initiation and the prey: *XY*–β′, *XZ*–β″, and *YZ*–β‴.

Reactive distance (RD) and its projections in the three planes: the distance between the fish's snout at a position just prior to the attack initiation and the prey: *XY–RD′*, *XZ–RD″*, and *YZ–RD‴*:

$$|\mathrm{RD}| = \sqrt{\mathrm{RD}'^2 + \mathrm{RD}''^2 + \mathrm{RD}'''^2}\ .$$

Capture angle (ε) in the three planes: the angle between the capture trajectory and the body axis prior to orientation: *XY*–ε′, *XZ*–ε″, and *YZ*–ε‴.

Capture distance (CD) and its projections in the three planes: the snout-to-snout distance between fish positions just prior to orientation to the prey and at capture: *XY–CD′*, *XZ–CD″*, and *YZ–CD‴*:

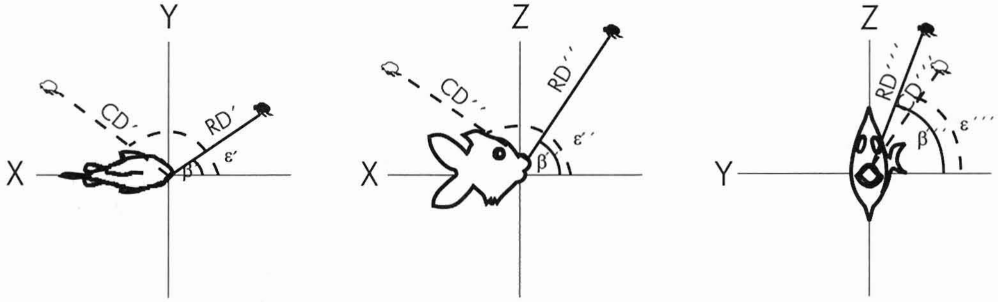
$$|\mathrm{CD}| = \sqrt{\mathrm{CD}'^2 + \mathrm{CD}''^2 + \mathrm{CD}'''^2}\ .$$

Visual resolution: expressed as visual angle (VA); with RD and the prey size (*h*), VA was estimated according to Hairston et al. (1982), Li et al. (1985), and Wanzenböck and Schiemer (1989):

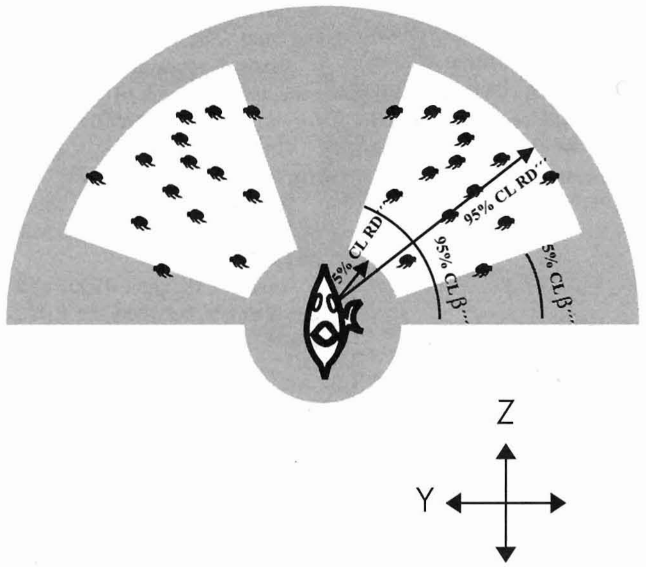
$$\mathrm{VA} = 2\left[ar\tan\left(0.5 \times \frac{h}{\mathrm{RD}}\right)\right].$$

Fig. 1. (*a*) Diagrammatic representation of the reactive distances (RD) and capture distances (CD) and reaction angles (β) and capture angles (ε) in the three space planes. Prey in black represent their positions at reaction, and prey in white, their positions at capture. The angle between the fish body axis and the prey position at reaction is β; the angle between the fish body axis and the prey positio at capture is ε. (*b*) View of the reaction field in the *YZ* plane. The white portions represent the area covering between the 5 and 95% confidence limits of the reactive distances (RD‴) and reaction angles (β‴). This area was multiplied by the fish's swimming speed to determinate its search volume (see text).

(a)



(b)



Search volume (SV)

For cruisers and sit-and-wait foragers, the SV can be calculated as the product of the CSp or the water velocity and the scanning area.

In the literature, there exists a variety of different methods for obtaining the scanning area (Confer et al. 1978; Dunbrack and Dill 1984; Wanzenböck and Schiemer 1989). From visual inspection, a rectangular scanning area (for example) appeared to be inappropriate. A circular area was not satisfying, as 0+ nase seldom reacted to prey situated below their horizontal plane. Another weakness of the published methods is that they ignore the blind region often found in front of the fish (see Braum 1964).

We thus applied a modification of the methods mentioned abov to delimit the scanning area. We used the 5 and 95% confidenc limits of the reactive distances and angles measured in th transversal plane (RD‴ and β‴), the inferior 5% to reflect the blin region just in front of the fish, and the superior 5% correspondin to unusual outliners (Fig. 1*b*).

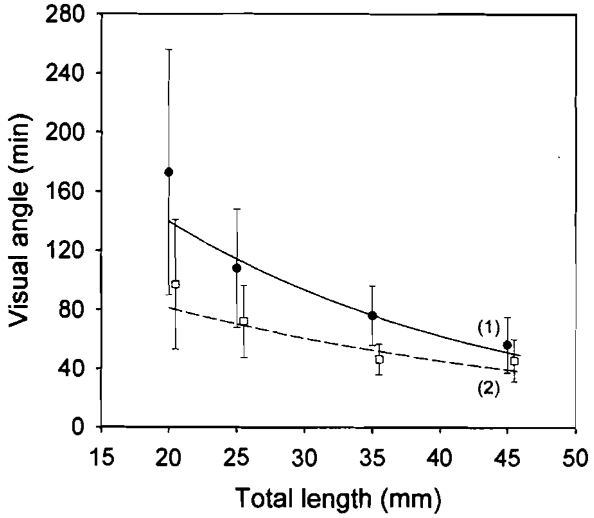
Results

The foraging mode of 0+ nase differed distinctly betwee calm water and flowing water. In calm water, young larva were mainly situated in the upper layer of the water colum

Table 1. Percentage of time spent in the three layers (upper, middle, lower) of the water column versus total length (TL) and water velocity (WV).

TL (mm)	WV ($cm{\cdot}s^{-1}$)	Water column layer: Upper	Middle	Lower
20	0.6	60	20	20
20	11	0	2	98
45	0.6	2	3	95
45	11	20	48	32

Fig. 2. Visual angle versus total length in calm (0.6 $cm{\cdot}s^{-1}$, circles) and flowing water (11 $cm{\cdot}s^{-1}$, squares). Data are means ± SD (n = 18). Regressions equations: (1) in calm water, VA = $309.10e^{(-0.36TL)}$, $r^2 = 0.57$, $n = 70$; (2) in flowing water, VA = $143.22e^{(-0.26TL)}$, $r^2 = 0.41$, $n = 70$.

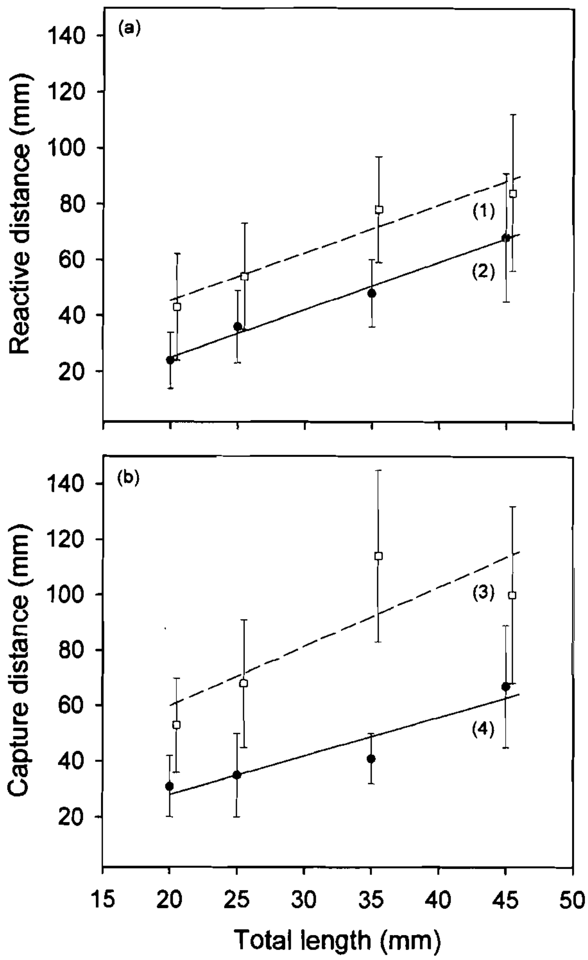


whereas later juveniles spent most of the time in the inferior layer (Table 1). Both size-classes adopted an active foraging mode, without pausing while searching for prey, and were therefore classified as cruisers. Between attacks in calm water, CSp significantly depended on fish size (one-way ANOVA, $P < 0.050$). CSp increased linearly with fish size (CSp = −1.85 + 0.22TL, $r^2 = 0.53$, $n = 180$, $P < 0.001$). In flowing water, young larvae of nase occupied mainly the inferior layer of the water column whereas later juveniles used the whole height of the water column. Both fish sizes showed a sit-and-wait behaviour. In this case, the fish's swimming speed between foraging attempts could be considered to equal the water velocity.

VA varied significantly with fish size and with water velocity (two-way ANOVA, $P < 0.001$). The relationship between VA and fish size could be described by negative exponential functions (in calm water: $P < 0.030$, in flowing water: $P < 0.042$) (Fig. 2). In three of the four size-classes, VA was significantly higher in still water than in flowing water (Tukey multiple comparisons, $P < 0.001$). The interaction term between fish size and water velocity was highly significant ($P < 0.001$).

RD and CD were significantly influenced by fish size and water velocity (two-way ANOVA, $P < 0.001$) (Figs. 3*a* and

Fig. 3. (*a*) Reactive distance and (*b*) capture distance versus total length (TL) in calm (0.6 $cm{\cdot}s^{-1}$, circles) and flowing water (11 $cm{\cdot}s^{-1}$, squares). Data are means ± SD (n = 18). Regressions equations: (1) in flowing water, RD = 1.11 + 0.17TL, $r^2 = 0.37$, $n = 70$; (2) in calm water, RD = −0.90 + 0.17TL, $r^2 = 0.54$, $n = 70$; (3) in flowing water, CD = 1.71 + 0.21TL, $r^2 = 0.33$, $n = 70$; (4) in calm water, CD = 0.04 + 0.14TL, $r^2 = 0.43$, $n = 70$.



3*b*). RD increased linearly with fish size in both calm and flowing water (in calm water: $P < 0.010$, in flowing water: $P < 0.050$). CD increased linearly with fish size in still water ($P < 0.050$).

In three of the four size-classes, RD values were significantly higher at 11 $cm{\cdot}s^{-1}$ than at 0.6 $cm{\cdot}s^{-1}$ (Tukey multiple comparisons, $P < 0.001$). CD was larger at 11 $cm{\cdot}s^{-1}$ in all size-classes (Tukey multiple comparisons, $P < 0.001$).

Means of the projections of RD and CD in the three planes varied significantly with water velocity and fish size (two-way ANOVA, $P < 0.001$). Water velocity had no effect on mean β values in the three planes (two-way ANOVA, $P > 0.050$). Mean β values in the *XZ* and *YZ* planes were dependent on fish size (two-way ANOVA, $P < 0.010$). Mean ε values in the *XY* and *XZ* planes were significantly influenced by water velocity (two-way ANOVA, $P < 0.010$). A summary of distances and angles of the reaction and capture fields in the three space planes is given in Table 2.

Positions of the prey at reaction and capture are represented in three dimensions in Fig. 4. Distributions of the re-

Table 2. Summary of the dimensions of the reaction and capture fields versus total length (TL) and water velocity (WV).

TL (mm)	WV ($cm \cdot s^{-1}$)	Reaction field	5% CL	95% CL	Mean	Capture field	5% CL	95% CL	Mean
20	0.6	RD′	0.8	3.9	2.2	CD′	0.9	4.1	2.5
		RD″	0.6	2.9	1.7	CD″	1.2	4.1	2.4
		RD‴	0.7	4	2.1	CD‴	1.3	4.2	2.4
		β′	0.4	149.3	62.7	ε′	6.1	141.5	61.9
		β″	13.5	151.4	58.4	ε″	18.7	144.7	63.1
		β‴	6	90	37.6	ε‴	10.5	82.8	47.2
20	11	RD′	0.6	6.5	3.2	CD′	1.6	7.5	4.8
		RD″	0.8	4.1	2.4	CD″	2.0	6.4	4.1
		RD‴	1.0	6.1	3.2	CD‴	0.9	5.9	3.2
		β′	13.4	90.0	50.5	ε′	94.2	175.0	140.9
		β″	14.1	90.0	50.1	ε″	99.8	178.3	149.6
		β‴	8.5	74.0	35	ε‴	3.9	81.7	34.7
45	0.6	RD′	1.9	7.7	4.8	CD′	1.4	8.5	4.3
		RD″	2.5	9.7	5.4	CD″	2.4	8.7	4.9
		RD‴	3.5	9.9	6.3	CD‴	3.6	9.9	6.1
		β′	4.1	100.1	57.7	ε′	23.8	121.6	69
		β″	21.2	99.8	64.9	ε″	37.8	122.7	74.9
		β‴	18.4	86.8	51.6	ε‴	17.7	85.1	50.3
45	11	RD′	1.3	11.5	5.7	CD′	2.6	13.7	7.8
		RD″	4.8	10.4	7.5	CD″	4.9	14.9	9.3
		RD‴	5.2	13.4	8.5	CD‴	5.4	13.2	8.7
		β′	4.1	90.0	58.1	ε′	105.7	165.6	137.4
		β″	50.7	90.0	69.7	ε″	103.2	151.9	125.9
		β‴	30.7	87.3	58.4	ε‴	28.4	80.6	55.8

Note: Values are given for the 5 and 95% confidence limits (CL) and the means in the three planes. Reactive distance (RD): *XY–RD′, XZ–RD″, YZ–RD‴*; capture distance (CD): *XY–CD′, XZ–CD″, YZ–CD‴*; reaction angle (β): *XY–β′, XZ–β″, YZ–β‴*; capture angle (ε): *XY–ε′, XZ–ε″, YZ–ε‴*.

action and capture points differed among calm and flowing water. In still water, the capture field approximately covered the reaction field in the fish's forward-oriented hemisphere. In contrast, the capture field at 11 $cm \cdot s^{-1}$ was clearly separated from the reaction field. The fish reacted to prey items positioned in their forward direction (between 0 and 90° in the *XY* and *XZ* planes with reference to the fish's snout at the beginning of the attack) and reached the drifting prey in their backward direction (between 90 and 180° with reference to the fish's snout at the beginning of the attack).

SV varied significantly with fish size and swimming speed (two-way ANOVA, $P < 0.001$) (Fig. 5). SV increased linearly with fish size ($P < 0.010$). SV was bigger in flowing water than in calm water for all size-classes (Tukey multiple comparisons, $P < 0.001$).

When calculated with the method of Eggers (1977), Confer et al. (1978), and Wanzenböck and Schiemer (1989), SVs of 0+ nase were 2–4.6 times larger than in our own calculations (Table 3).

Discussion

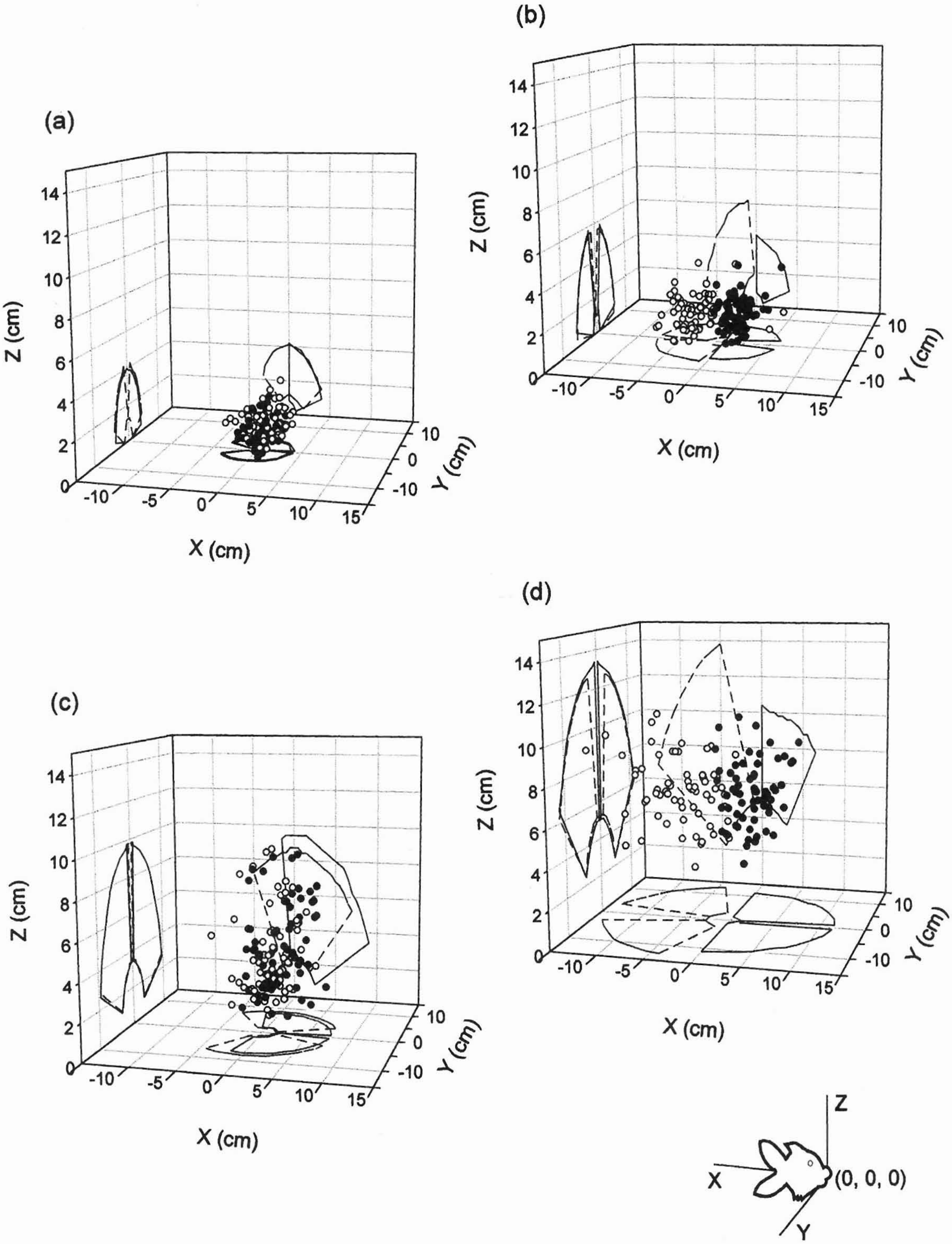
Following our observations, we recognized that 0+ nase in calm water used a cruise search strategy, without pausing to search for prey. They adopted a sit-and-wait foraging tactic in flowing water. When the average water velocity began to induce high size-dependent swimming costs (Flore and Keckeis 1998), individual nase were forced to migrate to the channel bottom where the water velocity is reduced. The average water velocity of 11 $cm \cdot s^{-1}$ was high enough to constrain the 20-mm nase in the lower water layer. At this water velocity, the 45-mm nase still used the whole height of water column.

RD of 0+ nase increased linearly with fish size. The improved visual performance during ontogeny is known to be correlated with processes of neuronal structural differentiation (Rahmann and Jeserich 1978). Also, the development of the eye and particularly the retina might be responsible for the enhancement of visual resolution (Li et al. 1985; Wanzenböck et al. 1996). Some authors also reported a linear increase in RD with fish size (Schmidt and O'Brien 1982; Wanzenböck and Schiemer 1989), but others found a nonlinear increase, being smaller for larger fish because the increase in eye size is counteracted by a decrease in cone density (Breck and Gitter 1983). In comparison with other fish species, visual resolution in 0+ nase is relatively high during early life stages and becomes weaker during later juvenile stages (Fig. 6).

RD was higher in flowing water than in still water. This finding implies that fish detected drifting prey in motion with the water velocity better than prey items suspended in calm water (Gendron and Staddon 1983; Wilzbach et al. 1986).

For the VA, we found a highly significant interaction term between fish size and water current. This indicates that the effect of water velocity was greater for smaller larvae and

Fig. 4. Three-dimensional representation of the reaction and capture fields of two size-classes of nase in calm and flowing water. (*a*) 20-mm nase at 0.6 cm·s^{-1}; (*b*) 20-mm nase at 11 cm·s^{-1}; (*c*) 45-mm nase at 0.6 cm·s^{-1}; (*d*) 45-mm nase at 11 cm·s^{-1}. Solid circle position of the prey at reaction; open circles, position of the prey at capture. The solid and broken lines determine the reaction area and capture area, respectively, in each space plane.



might reflect the poorer developmental stage of their eyes. The motion of the prey with the water current might thus play a more important role.

CD increased with fish size. In addition to the improvement in the visual system, the development of the swimming muscles and efficient propulsive movements during onto eny (Kaufmann 1990) allows the fish to swim faster a consequently to capture prey located at larger distances fro its position (Nyberg 1971). The 0+ nase covered larger C at higher water velocity. This was also observed by Gra

Fig. 5. Calculated search volume per time versus total length in calm (0.6 cm·s^{-1}, circles) and flowing water (11 cm·s^{-1}, squares). Data are means ± SD (n = 35). Regression equations: (1) in calm water, SV = –1975.90 + 101.29TL, r^2 = 0.72, n = 150; (2) in flowing water, SV + –2847.80 + 205.93TL, r^2 = 0.95, n = 119.

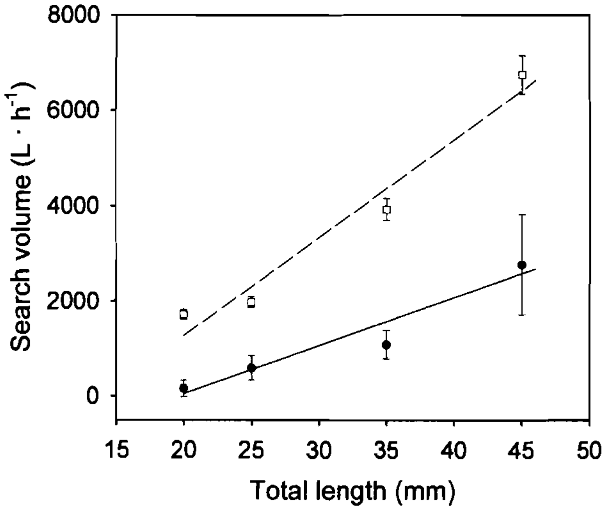


Table 3. Comparison of the mean search volume (SV) calculated with the method of Eggers (1977), Confer et al. (1978), and Wanzenböck and Schiemer (1989) (method *a*) and calculated with the present method (method *b*). TL, total length; WV, water velocity.

		Mean SV (L·h^{-1})	
TL (mm)	WV(cm·s^{-1})	Calculated with method *a*	Calculated with method *b*
20	0.6	345.4	157.1
	11.0	4672.5	1710
25	0.6	1519.5	593.1
	11.0	7065.5	1969.1
35	0.6	2887.8	1084.2
	11.0	17 435.2	3924.6
45	0.6	7986.9	2771.1
	11.0	22 327.2	6746.5

and Noakes (1987) for 0+ brook trout (*Salvelinus fontinalis*), but contrary results were also reported in the literature, e.g., for juvenile coho salmon (*Oncorhynchus kisutch*) and Atlantic salmon (*Salmo salar*) (Dunbrack and Dill 1984; Metcalfe et al. 1986; Godin and Rangley 1989) and adult Arctic grayling (O'Brien and Showalter 1993). Godin and Rangeley (1989) demonstrated that juvenile Atlantic salmon in increasing water current swam progressively shorter distances (CD) upstream to intercept drifting food items. The authors concluded that fish delayed capture further as the cost of swimming increased with increasing current velocity. Under natural conditions, cases have been reported where salmonids showed other patterns of foraging movements, e.g., by drifting and (or) swimming downstream with the current in pursuit of prey that had drifted past their stations (Streadmeyer and Thorpe 1987; Grant et al. 1989). Such patterns of capture were observed almost constantly in 0+ nase, pursuing their prey downstream and returning to their previous position near the stream bottom (Fig. 4).

Fig. 6. Comparison between visual angles of different species versus 1/standard length. Regression equations: (1) *Rutilus rutilus* (Wanzenböck and Schiemer 1989), VA = 20.03 + 3147.68SL^{-1}, r^2 = 0.94; (2) *Chondrostoma nasus* (present study), VA = –57.73 + 3552.34SL^{-1}, r^2 = 0.98; (3) *Abramis ballerus* (Wanzenböck and Schiemer 1989), VA = 44.82 + 1888.81SL^{-1}, r^2 = 0.88; (4) *Alburnus alburnus* (Wanzenböck and Schiemer 1989), VA = 27.52 + 1553.91SL^{-1}, r^2 = 0.88; (5) *Lepomis* spp. (Walton et al. 1994), VA = –3.58 + 1188.79SL^{-1}, r^2 = 0.99; (6) *Perca flavescens* (Wanzenböck et al. 1996), VA = –53.14 + 3038.49SL^{-1}, r^2 = 0.92.

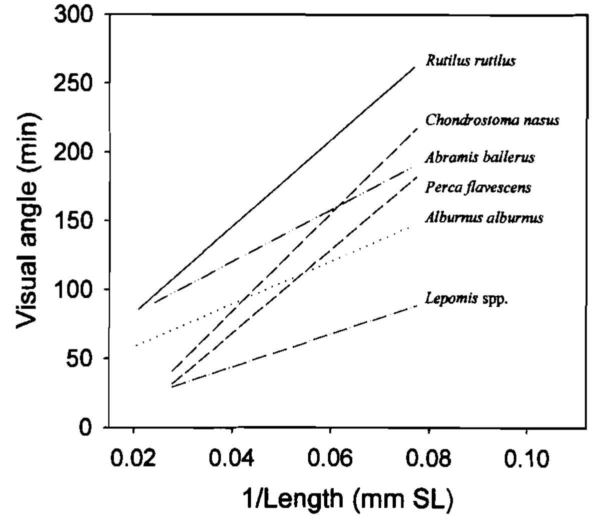
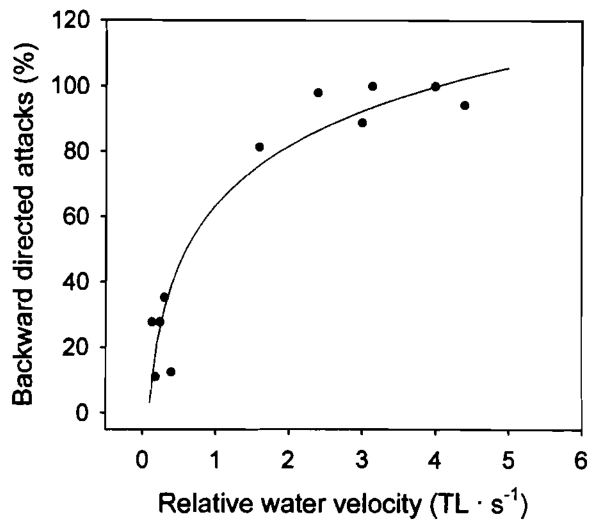


Fig. 7. Percentage of backward-directed attacks versus relative water velocity.



This pattern of foraging movements could be explained as (*i*) an alternative strategy that economizes swimming costs of prey capture in flowing water or (*ii*) the inability of 0+ nase to move out and intercept the prey before they are carried downstream of the feeding station, e.g., because of a lack of precision of the swimming direction up to the prey and (or) a bad evaluation of the distance and time required to reach the prey. We found a logarithmic relationship between the percentage of backward-directed captures and the relative water velocity (total lengths per second) (L. Flore, unpublished data). The percentage of backward-directed captures increased rapidly with a small increase in the relative water velocity and then reached a plateau at 100% (Fig. 7). Using the model of Kaufmann (1990), we roughly estimated the energy expenses per attack, based on calculations of their time budget and attack distance and direction. The 20-mm nase, for instance, showed swimming costs 1.9 times higher when they fed backward than when they fed forward (29.8 and 15.6 mJ·min^{-1}, respectively). The foraging mode of 0+ nase in flowing water might thus be the effect of a constraint imposed by water current rather than the result of an economic strategy.

The 0+ nase detected only low frequencies of prey directly in front of them. These results are consistent with the findings for bluegill (*Lepomis macrochirus*) (Luecke and O'Brien 1981), coho salmon (Dunbrack and Dill 1984), white crappie (*Pomoxis annularis*) (Wright and O'Brien 1984), roach (*Rutilus rutilus*), blue bream (*Abramis ballerus*), and bleak (*Albernus albernus*) (Wanzenböck and Shiemer 1989), and sunfish (*Lepomis* spp.) (Walton et al. 1994). Braum (1964) explained these low frequencies by a "blind region" in front of the larvae while searching for prey. Binocular vision is only achieved when the eyes are orientated forward. Even though their eyes are positioned laterally, the 0+ nase rarely reacted on prey situated in their caudal hemisphere, as observed for Arctic grayling (O'Brien and Evans 1992) and the sunfish (Walton et al. 1994). The prey captures that occurred below the horizontal plane represented only 4.7% of the total. This confirms that the investigated stages of nase were not yet benthic feeders. Reckendorfer et al. (1999) found mainly drifting invertebrates in the gut of 15- to 40-mm nase from the Danube River. Thetmeyer and Kils (1995) observed that herring were usually situated at 30–90° below their prey in the vertical plane. They demonstrated that this reflects a perfect strategy for the predator to stay invisible to the prey while the prey are fairly visible to the predator. The advantage of the predator to be invisible to the prey does not apply to the 0+ nase, considering that their characteristic species of prey show a very poor escape capability (Scott 1987). In contrast, prey located in the upper front sector could present an improved visibility to the 0+ nase (Janssen 1981).

The increase in SV of 0+ nase with increasing fish size was linear. Wanzenböck and Schiemer (1989) observed a logarithmic increase for 0+ roach, bleak, and blue bream. The modified method that we adopted for 0+ nase should provide an adequate estimation of their SV: (*i*) we deduced the lower half of the cylinder, as it comprises only a tiny proportion of the reactions, and (*ii*) we used the 5 and 95% confidence limits of the reactive distances and angles measured in the transversal plane (RD$'''$ and β'''), the inferior 5% to reflect the blind region just in front of the fish, and the superior 5% corresponding to unusual outliners (see Fig. 1*b*). When calculated with the method of Eggers (1977), Confer et al. (1978), and Wanzenböck and Schiemer (1989), SVs of 0+ nase in calm water were 2–4.6 times larger than in our own calculations. In Dunbrack and Dill (1984), the scanning area is estimated by multiplying the areas of each attack probability category by their corresponding attack probability and summing over all categories. However, this requires a larger number of observations. Also, it is not easily reproducible, since the shape of the areas of each probability was obtained by visual inspection. It is also important to stress that all calculations of SV based on measurements of RD underestimate the ability of fish to locate prey (Luecke and O'Brien 1981). RD probably represents the point at which a fish clearly recognizes prey as potential food and not the distance at which it can first see an object.

In conclusion, 0+ nase gain more advantage in foraging in flowing water rather than in calm water, referring to the larger volume searched for prey and associated encounter rate. Further parameters of foraging must, however, be taken into account. Prey capture success, attack rate, and consumption rate of 0+ nase drastically decline from a size-dependent critical water velocity (Flore and Keckeis 1998). Energetic expenses while swimming against the current increase exponentially with water velocity (Kaufmann 1990). Also, the capture of prey downstream is probably the result of a constraint imposed by the water current rather than an economic decision.

This information on the changes in the SV and capture field with fish size and water velocity may be helpful in determining microhabitat requirements of 0+ stages of nase and other rheophilic cyprinids with a similar foraging behaviour. Besides forced dislocations induced by water flows, microhabitat selection of 0+ rheophilic fish may ensue from identification of the benefits gained by spending time in a given foraging field and the costs incurred in the process in order to maximize net fitness gains.

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