

Ontogenetic changes in behavioural and histological measures of visual acuity in three species of fish

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Synopsis

Vision plays an important role in the early life history of fishes. We investigated the ontogenetic changes in visual acuity of early life history stages of alewife, *Alosa pseudoharengus*, yellow perch, *Perca flavescens* and bloater, *Coregonus hoyi*, across a range of sizes. Acuties were determined through histological examination of the retinae of larvae. Reactive distances of larvae to prey were estimated through videophotography of their response to prey and were then converted to measurements of visual angle. Both measures of visual ability improved with size (age) for all species. When behavioural and anatomical measures of ability were compared as a function of size, the data indicate that fish are anatomically more capable of seeing objects than the behavioural response suggests. In two of the three species, the relationship between histological acuity and visual angle was not constant. These results may indicate that while vision may limit initial rates of encounter and feeding, increases in visual acuity mean that in older stages limitations on encounter and feeding are more likely to be behavioural. Furthermore, these results indicate that encounter rates based upon histological estimates of visual acuity will be greater than comparable estimates based upon reactive distances. We recommend calculation of encounter rates based upon reactive distances.

Introduction

The acuity of fish visual systems improves during ontogeny (reviewed in Otten 1981, Blaxter 1986, Fernald 1991). These changes may lead to both increases in predator avoidance, due to an increased ability to detect potential predators (Gamble & Fuiman 1987, Batty 1989, Blaxter & Fuiman 1990), and to increased encounters with prey (Rosenthal & Hempel 1971, Blaxter & Staines 1971, Confer & Blades 1975, O'Brien 1979, Eggers 1977, Breck & Gitter 1983, Wright & O'Brien 1984,

Wanzenböck & Schiemer 1989, Browman & O'Brien 1992a, Walton et al. 1992). As fish larvae have a limited ability to withstand starvation (Miller et al. 1988) and feed on a resource that is patchily distributed and at low concentrations in the environment (Hunter 1981), factors which increase the rate of encounter will likely cause an increase in feeding rate. Regardless of whether fish employ an ambush, cruising, or pause-travel strategy, visual ability always enters theoretically-derived estimates of encounter rate as an exponential term (Gerritsen & Strickler 1977, Koopman 1980, Getty

& Pulliam 1991). Thus, improvements in visual acuity should translate into increased feeding success and reduced probabilities of starvation.

No single measure fully quantifies visual ability. Most frequently, visual ability is quantified using estimates of photopic acuity. This may be defined as the smallest angle which a stimulus may subtend at the eye and remain resolvable (Neave 1984). Photopic acuity may be estimated in two ways: anatomically and behaviourally. Anatomical estimates, here termed histological acuity, assume that a stimulus must excite at least two adjacent receptor cells to be resolved (Otten 1981) and may be quantified by measuring the density of cone receptor cells in the retina. Numerous studies indicate that the acuities of young fish, estimated histologically, improve steadily during their development (Blaxter & Jones 1967, Ahlbert 1976, Rahmann et al. 1979, Hairston et al. 1982, Breck & Gitter 1983, Neave 1984, Zaunreiter et al. 1991). The second frequently measured index of photopic acuity is reactive distance. Reactive distance is the distance at which fish respond behaviourally to the prey. If the size of prey attacked is known, simple trigonometric relations can be used to convert reactive distance measurements into estimates of acuity (Wanzenböck & Schiemer 1989). When measured in this manner, estimates of acuity also increase during development (Breck & Gitter 1983, Neave 1984, Wanzenböck & Schiemer 1989, Browman & O'Brien 1992a, b).

In this paper we consider two aspects of visual acuity in fishes – the relationship between histological acuity and reactive distance and how these two measures change during ontogeny. An appropriate comparison for the two measures of visual acuity is between histological acuity, the anatomical estimate of acuity, and visual angle, the behavioural expression of that physical ability. We also consider whether different species of fish of equal size have equal visual acuities. A general size-dependent relationship has been suggested by reviews of the literature (Blaxter 1986, Miller et al. 1988), but has not been supported in recent experimental investigations (Wanzenböck & Schiemer 1989, Zaunreiter et al. 1991).

Materials and methods

We investigated the visual acuity of three common Great Lakes fishes: alewife, *Alosa pseudoharengus*, yellow perch, *Perca flavescens* and bloater, *Coregonus hoyi*. These species are from different families and hatch at substantially different sizes: approximately 3.8 mm total length (TL, Heinrich 1981) for alewife; approximately 5.5 mm TL for yellow perch (Scott & Crossman 1973, Cucin & Faber 1985); and approximately 9.8 mm TL (Rice et al. 1987) for bloater. Experiments were conducted from May–September 1989 at the Center for Great Lakes studies, Milwaukee, Wisconsin. All fish used in experiments were raised in the laboratory from gametes obtained from natural populations. After hatching and start of exogenous feeding, larvae of all three species were transferred to fibreglass tanks, fed *Artemia* supplemented with frozen commercial feed, and maintained on a 12-h-light: 12-h-dark cycle at 12–15°C. Details of the rearing techniques are given in Miller et al. (1992).

Histological acuities were determined for fish of all three species from hatching to 40 mm TL following Neave's (1984) methodology. Ten fish of known age were sampled weekly from the rearing tanks, and measured for total length and eye diameter under a dissecting microscope. Individual fish were killed in a lethal concentration of MS222, fixed in full strength Zencker's solution for 1 h, and subsequently in 50% Zencker's solution for a further 2 h. Fish were then washed over-night and dehydrated in a graded alcohol series before final preservation in 100% ethanol. Individual fish were mounted in paraffin, sagittally sectioned at 3–5 μm through the left eye, and stained with eosin and haematoxylin for histological examination (Experimental Pathology Inc., Research Triangle Park, NC). Lens diameters were measured and cone cells were counted over six 100 μm retinal lengths through the widest point of the eye. Histological acuity, α ($^\circ$, or min of arc), was determined by:

$$\sin \alpha = \frac{0.0435}{d \cdot r} \quad (1)$$

where α is acuity, d is the cone density (# per

100 μm), and r (mm) is the radius of the lens, both corrected for shrinkage (Neave 1984). Shrinkage, approximately 10%, was calculated by comparing eye diameters of freshly killed and preserved individuals.

Reactive distances and their calculated visual angles were determined from video-taped foraging trials. All trials were conducted in 15 l rectangular tanks. Tank dimensions were $40 \times 20 \times 18.5$ cm. The tanks were lit from above by 'daylight' fluorescent lamps. Trials were conducted using *Artemia* nauplii at a prey concentration of 50 prey l^{-1} . All fish used in the trials had been fed *Artemia* for at least 5 days prior to a trial, and were starved for 24 h before a trial to standardize experimental conditions. Recordings were made for 5 min prior to the introduction of a ration to determine pre-feeding behaviour. Recordings continued for 15 min after the addition of food. All recordings were taken using a shadow photographic technique (Arnold & Nuttal-Smith 1974). Light from a 12V microscope bulb, controlled by a rheostat, was collimated by a lens before passing through the experimental tank. After passing through the tank, light was refocused by a second lens before entering the camera. Recordings were made using a video camera and recorder in both a vertical and horizontal orientation.

Video-recordings of all foraging trials were analyzed frame by frame using a personal computer based image-analysis system. Reactive distances were measured from the prey to the tip of the fish's snout from an image frozen at the instant the fish first oriented toward the intended prey. For each size class of each species we measured at least 20 reactive distances. We also recorded whether an attack resulted in a prey capture. To permit direct comparisons among trials, and with histological measures of visual acuity, we transformed the measured reactive distances into visual angles (VA) using the following relationship:

$$\text{VA (min of arc)} = 2 \cdot (\tan^{-1}(h/2 \cdot \text{RD})) \quad (2)$$

where h is the mean dimension (mm) of the prey presented to the fish and RD is the reactive distance (mm) of the fish (Wanzenböck & Schiemer

1989). The mean dimension of *Artemia* nauplii used in these experiments was 0.38 mm. In subsequent analyses, mean values ($n > 20$) of RD and VA are used.

All data were analyzed for the degree of fit to simple linear and logarithmic functions of fish total length, λ , using appropriately transformed data in an analysis of covariance. The relationships with the highest R^2 are reported here.

Results

The visual system of all three species changed as fish grew. Lens diameters ($= 2 \cdot r$, where r = lens radius defined in equation 1) increased linearly with size for each species (alewife lens diameter (mm) = $0.029 \cdot \lambda - 0.14$, $R^2 = 0.93$, $n = 17$, $p < 0.001$; yellow perch lens diameter (mm) = $0.034 \cdot \lambda + 0.029$, $R^2 = 0.95$, $n = 56$, $p < 0.001$, and; bloater lens diameter (mm) = $0.025 \cdot \lambda - 0.06$, $R^2 = 0.96$, $n = 13$, $p < 0.001$). Lens diameter data were coupled with retinal cone cell counts to estimate histological acuities using equation 1. All histological estimates of visual acuity improved as fish grew. Histological acuities exhibited size-dependent relationships and decreased non-linearly during ontogeny in all three species (Fig. 1). Estimates of histological acuity were fitted to both exponential and hyperbolic relationships. Hyperbolic models explained more of the variance than the exponential models. Differences among the slope or intercepts of the relationships for the three species were insignificant (ANCOVA $p > 0.05$; Table 1), so a single size-dependent relationship based on the observations from the three species was therefore fitted to the data (Fig. 1).

Reactive distances, the behavioural measure of visual acuity, increased linearly with fish size for all three species (Fig. 2a). As with histological acuity, analysis of covariance showed a clear size effect, but failed to detect a significant difference either in the slopes or intercepts of the species-based relationships (Table 1). This suggests that reactive distance can be described by a single size-dependent relationship of the form $\text{RD (mm)} = 0.97 + 0.47 \cdot \lambda$, $R^2 = 0.78$, $n = 12$, $p < 0.001$. There was no

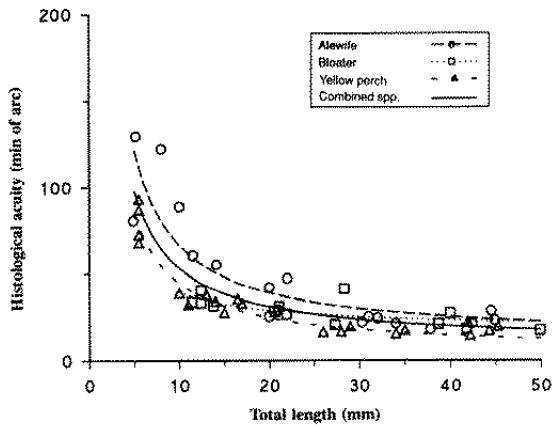


Fig. 1. Measures of histological acuity (min of arc) as a function of fish size (mm). Note that lower values of acuity indicate better vision. Regression relationships are: alewife $\alpha = 11.39 + 551.23/\lambda$, $R^2 = 0.76$, $n = 13$, $p < 0.001$; bloater $\alpha = 17.99 + 215.08/\lambda$, $R^2 = 0.45$, $n = 13$, $p < 0.001$; yellow perch $\alpha = 4.53 + 400.9/\lambda$, $R^2 = 0.93$, $n = 17$, $p < 0.001$; and; combined species $\alpha = 8.65 + 446.53/\lambda$, $R^2 = 0.72$, $n = 47$, $p < 0.001$.

significant difference in the reactive distance of successful versus unsuccessful attacks for any species or any size of fish. Attack success is therefore

Table 1. Summary of analysis of variance results of some estimates of visual acuity. Analyses were conducted with size as gradient treatment. The values reported are for the best fit to either a linear size-dependent relationship or a logarithmic size-dependent relationship.

Source	df	SS	p
(i) Histological acuity			
Species	2	0.0004	0.24
Size	1	0.002	0.0001
Size \times species	2	0.0002	0.15
Error	46	0.0027	
(ii) Reactive distance			
Species	2	21.29	0.34
Size	1	322.07	0.0008
Size \times species	2	9.29	0.59
Error	6	23.94	
(iii) Ln (visual angle)			
Species	2	0.56	0.06
Size	1	2.55	0.0007
Size \times species	2	0.30	0.17
Error	6	0.38	

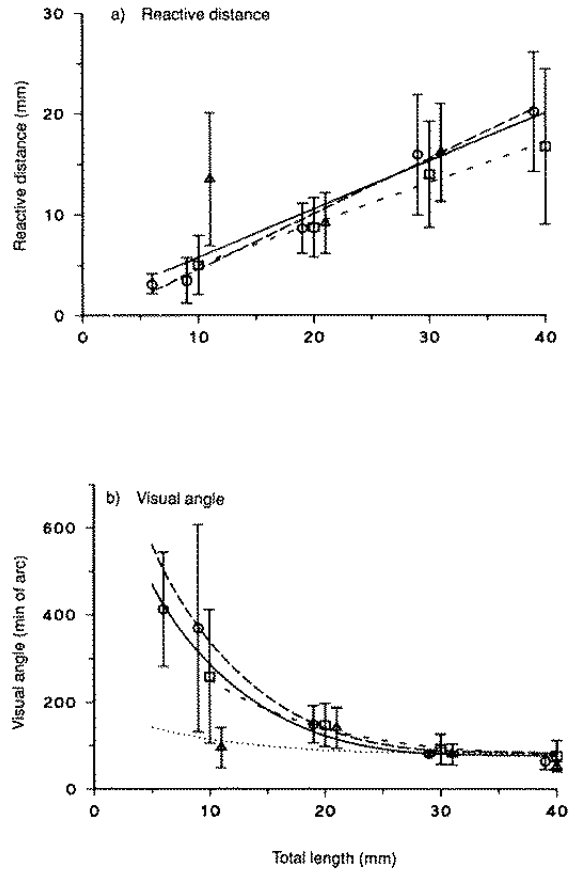


Fig. 2. Behavioural measures of visual ability of fishes as a function of fish size. Symbols as in Figure 1. For clarity alewife data are plotted at 1 mm smaller, and yellow perch at 1 mm larger than the real fish lengths. The regression relationships are however not adjusted. a – reactive distance (mm, \pm s.e.m.). Regression relationships were: alewife RD (mm) = $0.55 \cdot \lambda - 1.45$, $R^2 = 0.99$, $n = 4$, $p < 0.01$; bloater RD (mm) = $0.40 \cdot \lambda + 0.98$, $R^2 = 0.99$, $n = 4$, $p < 0.01$; yellow perch RD (mm) = $0.41 \cdot \lambda + 5.64$, $R^2 = 0.63$, $n = 4$, $p < 0.01$; b – visual angle (min of arc, \pm s.e.m.). Regression relationships are: alewife VA = $3218/\lambda - 10.36$, $R^2 = 0.96$, $n = 5$, $p < 0.05$; bloater VA = $16.92 + 2441/\lambda$, $R^2 = 0.99$, $n = 4$, $p < 0.02$; yellow perch VA = $71.09 + 408/\lambda$, $R^2 = 0.13$, $n = 4$, n.s., and; combined taxa VA = $1.25 + 2657/\lambda$, $R^2 = 0.75$, $n = 13$, $p < 0.07$.

determined after the commitment to the attack is made. Visual angles also showed clear size-dependent relationships (Fig. 2b, Table 1). Analysis of covariance indicated a significant size effect, but did not detect a significant species specific difference among measures of visual angle. However, the test for a species effect is only marginally in-

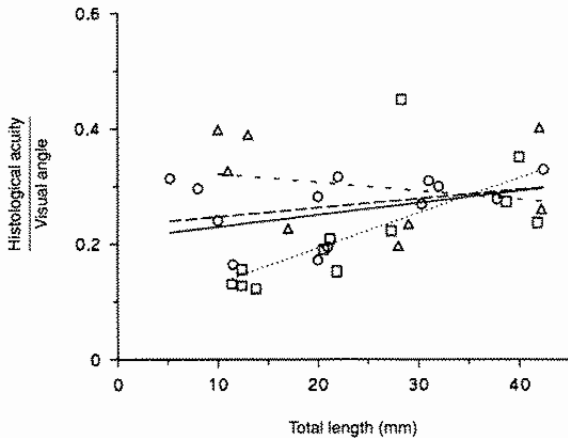


Fig. 3. Comparison of visual ability (min of arc) as measured by histological (acuity) and behavioural (visual angle) observations as a function of fish size. Symbols as in Figure 1. Regression equations are: alewife-ratio = $0.0015 \cdot \lambda + 0.231$, $R^2 = 0.32$, $n = 12$; bloater-ratio = $0.006 \cdot \lambda + 0.07$, $R^2 = 0.69$, $n = 12$, and; yellow perch-ratio = $-0.0015\lambda + 0.336$, $R^2 = 0.23$, $n = 12$.

significant. The data for the three species were used to develop a general size-dependent relationship yielding; VA (min of arc) = $1.247 + 2657/\lambda$, $R^2 = 0.75$, $n = 13$, $p > 0.07$.

To relate anatomical and behavioural estimates of visual ability we compared the histological acuities of a sample of fish from the rearing tank to the mean reactive distances of a similar sample of fish (Fig. 3). The relationship between histological acuity and visual angle at any one size is a direct comparison of the physical ability of a fish to see and the behavioural expression of that ability. When measures of these two estimates are compared, it is apparent that the behaviourally obtained estimate, visual angle, is considerably larger than the anatomically obtained estimate, histological acuity, i.e. $\alpha/VA \ll 1$. To investigate the relationship between the two estimates of acuity we plotted the ratio of visual angle: histological acuity as a function of size for individual species. For bloater and alewife the slope of this relationship is significantly non-zero; alewife $t = 2.14$, $p < 0.05$; bloater $t = 2.96$, $p < 0.05$. This is not the case in yellow perch, where the slope of the ratio-size relationship did not differ significantly from zero ($t = -0.58$, n.s.).

Discussion

In laboratory studies, we investigated the ontogeny of and the relationship between the physical ability of individual fish to detect prey (histological acuity) and the behavioural expression of that ability (reactive distance and visual angle). This knowledge should improve our understanding of the role of visual acuity in regulating the encounter rate and hence foraging ability of fish larvae and juveniles. We also examined the notion that considerations of body size scaling would assist in reconciling species-specific differences in visual ability in fish larvae and juveniles.

The visual acuities, whether measured histologically or behaviourally, of all three species were non-linear functions of size. This suggests that the ability of these fish to see the same prey further away or smaller prey at the same distance should increase as they grow. Similar relationships have been reported for, amongst others, centrachids (Breck & Gitter 1983, Li et al. 1985), clupeids (Blaxter & Jones 1967, Sandy & Blaxter 1980), cyprinids (Hairston et al. 1982, Zaunreiter et al. 1991), salmonids (Ahlbert 1976, Rahmann et al. 1979) and several flatfish (Sandy & Blaxter 1980, Neave 1984).

Reactive distance is the most common behavioural measure of visual ability. It may be defined as the distance between the prey and the fish when the fish responds to the potential prey. Reactive distances of all three species were well described by a common linear size-dependent relationship, and no significant species effect was detected. The three species used in our study span $> 80\%$ of the size range of pelagic marine and freshwater fish embryos at hatching (Miller et al. 1988). Although they differed substantially in morphology, they do not fully reflect the variety of morphologies found in fishes in general (Moser 1981) and thus they may not represent an extreme test for a species effect. The linear size-dependent relationship we report is supported by other studies. Blaxter & Staines (1971) report linear age-dependent relationships for three species of marine fishes. Wanzenböck & Schiemer (1989) found linear size-dependent relationships for reactive distance for three European

cyprinid species. However, one of the species they studied differed significantly from the other two, both in terms of the slope and the intercept of the regression relationship. Wanzenböck & Schiemer attributed this difference to the different foraging modes of the three species studied.

When we compared anatomical estimates (histological acuity) to our behavioural estimates (visual angle) the histological estimate was always more acute than the behavioural estimate. Li et al. (1985) report similar findings for bluegill sunfish *Lepomis macrochirus*, yet Breck & Gitter (1983) indicate that for larger bluegills, behavioural and anatomical estimates of visual ability are similar. Browman et al. (1990) compared histological and behavioural estimates of visual acuity in white crappie, *Pomoxis annularis*, and also found that behavioural estimates of visual angle were greater than histological estimates. There are several possible explanations for the discrepancy between the histological and behavioural estimates of visual ability in fish larvae.

Behavioural estimates may underestimate visual acuities since fish may not respond to the limit of their visual ability. O'Brien et al. (1990) have suggested that behavioural estimates may be biased as a result of the foraging strategy employed by fish. They suggest that many fish use a pause-travel or saltatory search strategy and only search their visual field when they are stationary. If no prey are seen the fish moves, stops and rescans. For any one scan of the visual field prey may be anywhere in the field. Thus the distance from the fish to an observed prey is a random variable, limited by the maximum reactive distance. Therefore the mean observed reactive distances will underestimate visual acuity (see O'Brien et al. 1990, Browman & O'Brien 1992a, b for further discussion). Another potential bias is that the light and contrast conditions in our experimental system may not have allowed the fish to exhibit their full potential reactive distance. Additionally, we allowed the fish to feed on a prey assemblage, not on single prey introduced individually into the tank. Both features may have reduced our estimates of reactive distance.

Alternatively, histological acuity may overesti-

mate visual acuity. Histological acuity may not accurately reflect the sensitivity of a fish's vision as it assumes stimulation of only two adjacent cone cells is necessary for prey recognition (Otten 1981). If one assumes that the reactive distance of larvae represents the limit of their visual ability, our data suggest that, for example in a 10 mm larvae, it is necessary for 5 cone cells to be stimulated for a prey to be detected. The possibility that histologically-based estimates are biased is supported by Zaunreiter et al. (1991) who demonstrated that the convergence of photoreceptors onto ganglion cells increases during ontogeny. However, as the visual angles are greater than histological acuity, it appears that, in young fish, there is a distance over which the fish can see prey, but do not initiate an attack. This latent segment is difficult to measure behaviourally and therefore presents a problem in operationally defining terms to test alternative encounter models (e.g., O'Brien et al. 1976, Eggers 1982).

To investigate these patterns further, we compared physical and behavioural estimates of visual acuity. We assumed that our histological and behavioural estimates of acuity show no pattern of bias as a function of fish size, that is they are a constant proportion of their 'true' value. For pause-travel foragers, mean reactive distance underestimates visual acuity (O'Brien et al. 1990, Browman & O'Brien 1992a). However, as reactive distance is a random variable, the mean value and any higher moment of the distribution will be strongly correlated (Bailey 1971). Thus the pattern of any size-dependent relationship will be robust regardless of whether one considers the estimates of the mean or the 90th percentile. Using mean reactive distances in comparing size-dependencies will not bias our results, even in the case of pause-travel forager. If visual acuity is an important constraint on encounter probabilities and feeding success, then as visual acuity improves, we would expect the same improvement in its behavioural estimator, visual angle. Under these conditions we hypothesize that the ratio of histological acuity : visual angle will be constant. However, if acuity is not a constraint, we would expect the two estimates to be uncoupled. For two of the three species, alewife and bloater,

we could reject the null hypothesis. The rejection of this null hypothesis has two potential implications. One interpretation is that visual acuity is not a constraint on feeding ability. This interpretation suggests future research should focus on identifying which factors do constrain feeding and how these constraints change during ontogeny. We suggest that behavioural components of predation such as reaction time and burst swimming speed, or features of prey behaviour such as movement rather than visual acuity constrain foraging behaviour. An alternative explanation would be that our estimates of histological or behavioural acuity are biased and the non-zero slope of the ratio of the two acuities reflects perhaps changes in retinal convergence (Zaunreiter et al. 1991), sampling error due to differences in cone cell density and hence histological acuity over individual retinæ (Browman & O'Brien 1992a), or experimental artifacts restricting the full behavioural expression of visual acuity.

To investigate this pattern further we compared physical and behavioural estimates of visual ability from this study and data developed in other studies (Fig. 4). In all cases, behavioural estimates were poorer than physical estimates of visual ability. These data support the notion that behavioural estimates of visual acuity underestimate the physical ability of fish to see. Furthermore, there is a strong, general size-dependent relationship for visual ability, whether it is estimated behaviourally or anatomically. It seems that there are commonalities in the development of visual ability in fish larvae and juveniles (Blaxter 1986), that allow size to serve as an appropriate scaling factor. This would suggest that one may be able to predict the visual ability of a relatively unstudied species based on the existing data from well studied species. However, we caution that such an approach would represent only a first approximation.

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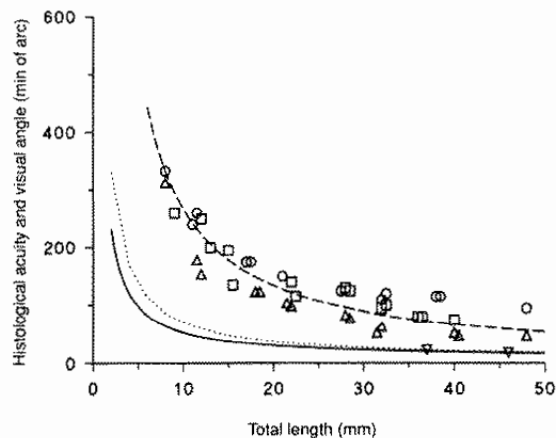


Fig. 4. Comparison of estimate of visual ability (min of arc.). Symbols are: histological acuity – this study —; visual angle – this study ---; histological acuity (Breck & Gitter 1983, and Hairston et al. 1982) ...; mean visual angle, Hairston et al. 1982 – bluegill ∇ ; visual angle, Wanzenböck & Schiemer 1989 – roach \circ ; visual angle, Wanzenböck & Schiemer 1989 – bleak \square , and visual angle, Wanzenböck & Schiemer 1989 – bream \triangle .

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