

STALKED EYES AS AN ADAPTATION TOWARDS MORE
EFFICIENT FORAGING IN MARINE FISH LARVAE*D. Weihs and H. G. Moser*

A B S T R A C T

The development of stalked eyes in the larvae of some midwater marine fish species is studied. Our mathematical analysis suggests that this adaptation results in an increase in feeding efficiency.

The larvae of most marine fish species, including benthic ones, live in the upper mixed layer of the ocean where primary and secondary production is high and where competition for the available food particles, as well as the chances of predation on the larvae, are great. The myriad morphological, physiological and behavioral adaptations these larvae have evolved for survival in this environment have only recently begun to be understood (Blaxter, 1974).

Among the more remarkable adaptations are those involving the eye. Larvae of certain groups of midwater salmoniform and myctophiform families have larvae with markedly narrowed, elliptically shaped eyes, and in some of these species the eyes are borne on stalks (Fig. 1, Table 1). The possible significance of narrowed and stalked eyes has not been examined to date. Since they have evolved independently in phylogenetically distinct orders, it seems likely that they are adaptive and it is the purpose of this note to suggest some possible advantages of these adaptations. Stalks vary in length from cases where the medial surface of the eye lies just outside the surface of the head, to quite long, as in the Idiacanthidae where they reach a length greater than $\frac{1}{4}$ of the body length and are supported by a cartilaginous rod (Brauer, 1908; Beebe, 1934). In bathylagids (Tåning, 1931) and myctophids (Moser and Ahlstrom, 1970; 1974) there is a complete range of conditions from species with round sessile eyes, to species with elliptical sessile eyes, to species with stalks of various lengths. Where the phenomenon occurs in eels (Smith, 1979), the eyes are not on slender stalks but protrude within an envelope of skin and are more appropriately called telescopic. In some species with narrow-eyed larvae (Table 1), particularly in the Myctophidae and Scopelarchidae, a lunate to conical mass of tissue is attached to the ventral surface of the eye. It is part of the chorioid layer of the eye and may function during metamorphosis when the eye must enlarge rapidly and become round (Moser and Ahlstrom, 1970).

The major causes of larval fish mortality are starvation and predation and interactions between them (Hunter, 1976). Feeding and predator avoidance are largely dependent on vision and eye specializations to improve these can therefore be expected. Sighting distance and visual field are major limitations for feeding larvae. Hunter (1972) showed that anchovy larvae notice and strike at food particles positioned within a 60° cone parallel to the body axis with maximum height of about one body length (10 mm). Similar behavior is known for larvae of *Coregonus* and *Esox* (Blaxter and Staines, 1971). As suggested by Moser and Ahlstrom (1970), increase in rotational ability around the long axis of the eye would enlarge the observable volume available from a given point. Extension of the eyes on stalks would further enlarge this volume. This raises the possibility of

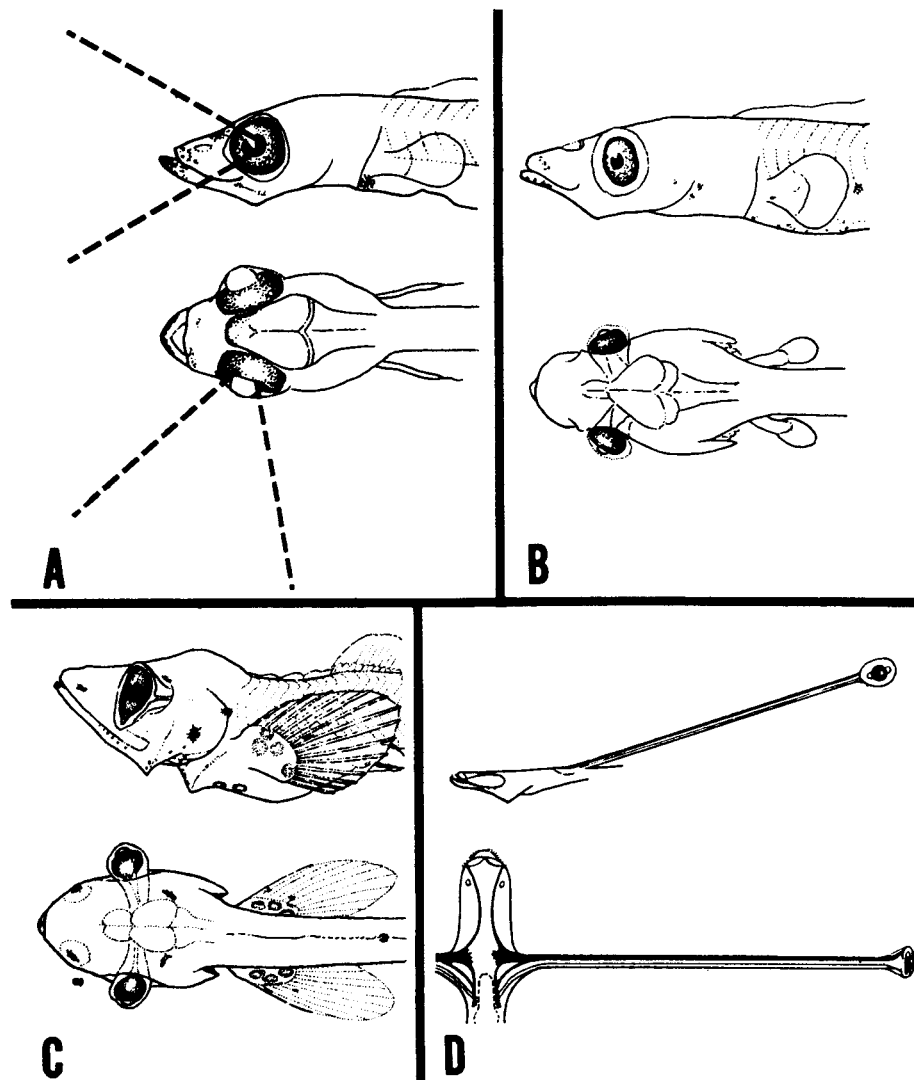


Figure 1. Various eye shapes of marine teleost larvae. A, Round eye—*Bathylagus milleri*, lateral view (above) of 10.6-mm larva; dorsal view (below) of 9.5-mm larva; B, Narrow sessile eye—*Bathylagus wesethi*, lateral view of 8.8-mm larva; dorsal view of 8.5-mm larva; C, Narrow slightly stalked eye of 7.0-mm *Myctophum nitidulum* larva (after Moser and Ahlstrom, 1970); D, Markedly stalked eyes of 16-mm *Idiacanthus fasciola* larva (after Beebe, 1934).

detecting prey from greater distances with a minimum of body motion, thus both conserving energy and reducing the probability of attracting the attention of predators (Lillelund and Lasker, 1971).

We propose that enlargement of the visual field has evolved progressively through several stages. The first stage would be a narrowing of a sessile round

Table 1. Occurrence of elliptical and stalked eyes in larvae of teleost fishes. "++" indicates presence of character in taxon and "++" indicates that the character state is widespread in taxon

Taxon	Elliptical Eyes	Ventral Choroid Tissue	Stalked Eyes
Anguilliformes			
Congridae	++	+	short
Xenocongridae	++	+	short
Synphobranchidae	++	0	short
Notacanthiformes			
	+	+	short
Salmoniformes			
Argentinoidei			
Bathylagidae	++	0	short to long
Stomiatoidei			
Gonostomatidae	+	0	short
Sternoptychidae	++	0	0
Chauliodontidae	+	0	short
Stomiidae	+	0	short
Astronesthidae	+	0	short
Melanostomiidae	+	0	short
Malacosteidae	+	0	short
Idiacanthidae	+	0	long
Myctophiformes			
Notosudidae	++	0	0
Myctophidae	++	+	short to long
Evermannellidae	++	+	0
Scopelarchidae	++	+	0
Perciformes			
Labridae	+	+	0
Scaridae	+	+	0

eye. Genera and species with narrow and slightly protruding elliptical eyes (Fig. 1B) are common in all the groups which have stalk-eyed larvae (Table 1). The next stage would be the extension of the eyes on short stalks so that they lie just outside the margin of the head (Fig. 1C). Such an eye could presumably rotate freely, in contrast to a round cup-shaped eye which lies flat in the developing orbit. Numerous examples of such stalked eyes are found in the Bathylagidae, in the stomiatoid families and in the Myctophidae. The final stage, where the eyes are borne on pedunculate stalks of various lengths, is found in the Bathylagidae, Idiacanthidae and Myctophidae (Fig. 1D).

To examine the hypothesis of increased visual field quantitatively, we first assume the visual perception distance d (Fig. 2) to be equivalent in stalked or unstalked eyes. The volume observable, V , by a single unstalked eye is obtained from

$$V = \int_0^{\psi_1} \int_0^{\theta_1} \int_0^d r^2 \sin \theta \, dr \, d\theta \, d\psi = \psi_1 (1 - \cos \theta_1) \frac{d^3}{3} \quad (1)$$

where r , θ , ψ are spherical coordinates (Moon and Spencer, 1971, or any Vector analysis textbook), and ψ_1 , θ_1 are the field cone angles in radians in the azimuthal and vertical directions, respectively. (When $\theta = \pi$ and $\psi = 2\pi$, equation (1) leads to the formula for the sphere volume $V = 4\pi \frac{d^3}{3}$.) For Hunter's (1972) data

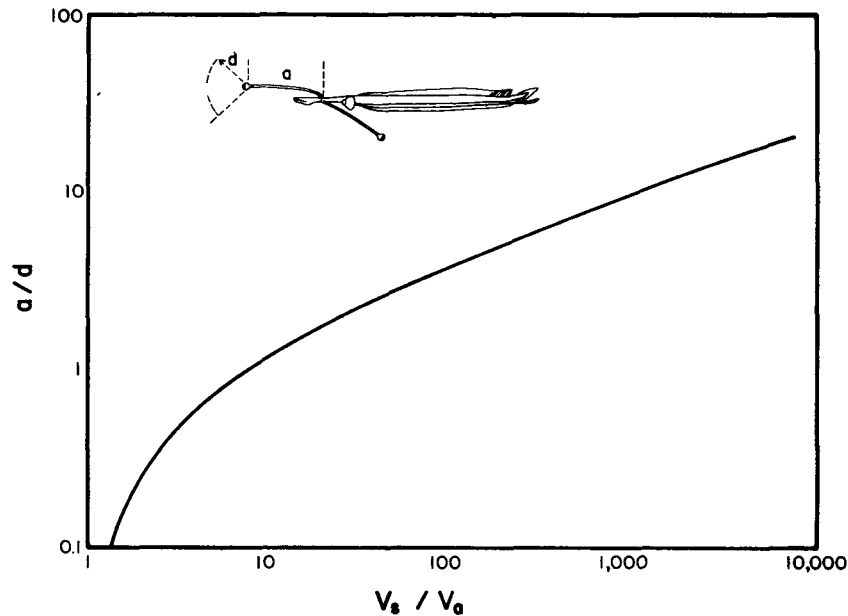


Figure 2. Ratio of the volume sighted by stalked eyes V_s , to that covered by fully rotatable eyes attached to the head V_a , versus the ratio of stalk length a to perception distance d . *Idiacanthus* larva is shown to illustrate the geometrical parameters.

($\theta_1 = \psi_1 \approx \frac{\pi}{3}$) the volume covered by both eyes is

$$V = 2 \frac{\pi}{3} \left(1 - \frac{1}{2}\right) \frac{d^3}{3} = \frac{\pi}{9} d^3. \quad (2)$$

The volume is approximately 8% of the volume of the sphere of radius d . Any adaptation towards freely rotatable eyes (as in the chameleon), which enables the volume observed to approach the spherical shape, would be a significant improvement. Improved eye rotation in fish larvae with elliptical eyes seems highly likely, but confirmation must await future field or aquarium observations.

The visual field of larvae with stalks is examined next. In eye stalks of preserved *Idiacanthus* larvae the supporting cartilaginous rod is rather stiff but pliable with more flexible hinge points at the attachment to the head and eyeball. The extrinsic eye muscles pass along the posterior surface of the rod and fan out to their points of origin and insertion at either end. The structure suggests that the stalks may be freely waved or flexed and that the eyeball itself may be rotated in two planes to the extent that the larva can look back at itself. With this assumption, if stalk length is a , the volume covered by both eyes V_s is spherical, with radius $a + d$. This can be compared to the visual volume of fully rotatable eyes with no stalks by writing the ratio of volumes covered

$$\frac{V_s}{V_a} = \frac{4}{3}\pi(a + d)^3 / \frac{4}{3}\pi d^3 = \left(1 + \frac{a}{d}\right)^3 \quad (3)$$

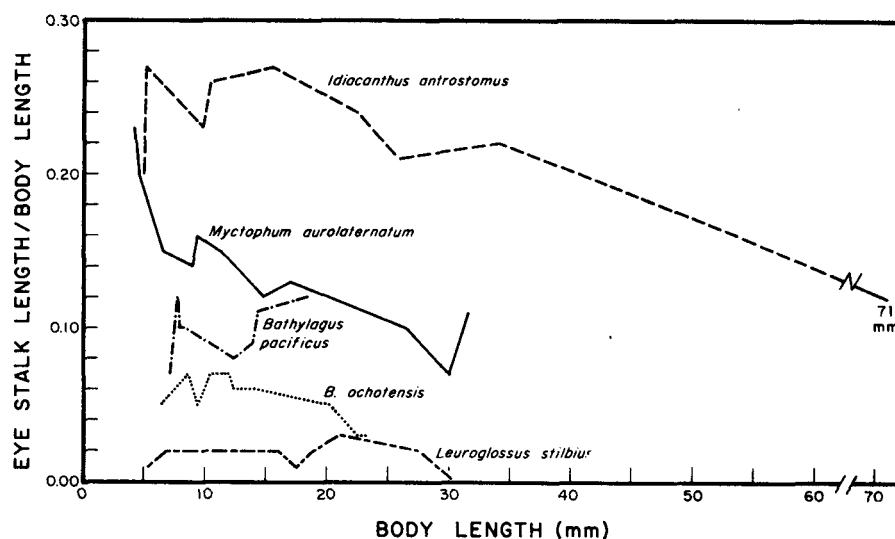


Figure 3. Ratio of eye-stalk length to body length, versus body length for larvae of five species.

The values of this ratio, as a function of a/d are shown in Figure 2. The increase in volume covered is enormous, especially for relatively long stalks (large a/d). The visual perception distance is assumed to be similar for all larvae, so that we can apply Hunter's (1972) perception distances. This distance seems to level off for larvae of more than 12 mm body length with $d \leq 10$ mm. We take the maximum value $d = 10$ mm, since the striking distance for smaller larvae may not be related to perception distance. In any case, this choice is conservative as it results in an underestimate of the increase in visual field due to eye motility. We now combine this with values of a in Figure 3 to obtain the ratio a/d required in Figure 2. For example, *Idiacanthus*, at 44 mm length, had stalks of over 9 mm length, i.e., $\frac{a}{d} \approx 0.9$ and $\frac{V_s}{V_a} \approx 7$, so that the total volume covered by this species of stalked larva is over 80 times that of an equivalent larva, i.e., of similar size and optical acuity, with fixed non-rotatable eyes.

This immense increase in observable range, therefore, indicates a potential for a large increase in feeding efficiency, defined as the ratio of energy intake to energy expenditure in finding the food (Weihs, 1975), by increasing the foraging effectiveness. This is a special advantage in areas of low food density, where rather long searches may be required for each prey particle of appropriate size. It is expected that the eyes would be manipulated to follow the prey during the approach stage, so as to decrease the probability of a missed capture.

Eye-stalk motions as an alternative to swimming would also reduce the disturbance to the surrounding water mass, which is a result of the transfer of energy from larvae to the water by viscous drag effects. As a result, pressure signals, which could attract predators (or warn prey), are reduced and the chance for survival is further increased. These advantages are large enough to compensate for the evolutionary investment in the growing of stalks which are resorbed at

later stages. Actually, the tenfold increase in sighting volume made possible by just enabling non-stalked eyes to rotate, strengthens our assumption that even narrowed eyes, as in Figure 1B, are shaped for increased searching capability. This results from the observation that the narrow eyes are embedded in a larger hemispherical depression (Fig. 1B) so that the additional space is available for the postulated rotation. The energy required for moving the eyes is much smaller than that of moving the whole body.

Behavioral observations of the types of larvae mentioned here have not been reported. We hope that the present predictions will lead to increased interest and further understanding of these fascinating adaptations.

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