

## Changes in the refractive state during prey capture under low light in the nocturnal cardinalfish *Apogon annularis*

Roi Holzman<sup>a,b,\*</sup>, Nadav Shashar<sup>a,b</sup>, Howard C. Howland<sup>c</sup>, Gadi Katzir<sup>d</sup>

<sup>a</sup> The Interuniversity Institute for Marine Sciences in Eilat, P.O. Box 469, 88103 Eilat, Israel

<sup>b</sup> The Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, P.O. Box 469, 88103 Eilat, Israel

<sup>c</sup> Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, 14853, USA

<sup>d</sup> Department of Biology, Oranim – Haifa University, Tivon 36006, Israel

Received 30 May 2005; received in revised form 6 October 2005

### Abstract

Many nocturnal and crepuscular fish use vision to feed and function under low light levels. However, little is known about their ability to accommodate or their visual acuity under these light levels. We used Infrared Photoretinoscopy to track the refractive state of the eye during prey capture under low light in *Apogon annularis*, a nocturnal reef fish. Anatomical measurements of the eyes allowed calculations of visual acuity. Changes in the refractive state were observed in ~75% of the prey capturing strikes, preceding the strikes by 30 ms. These changes were rare between strikes or when prey was absent. Anatomical measurements indicated that the number of photo-detection units in a retinal image greatly exceeded the minimal number needed to detect prey. We conclude that nocturnal vision in *A. annularis* is sufficiently sensitive to allow accommodation during prey capture.

© 2006 Elsevier Ltd. All rights reserved.

**Keywords:** Nocturnal vision; Resolution; Sensitivity; Scotopic vision

### 1. Introduction

Vision is a dominant modality among diurnal and crepuscular fishes in shallow aquatic habitats (Blaxter, 1980; Lythgoe, 1979; McFarland, 1991; O'Brien, 1987). It is employed in activities ranging from foraging and predator–prey interactions, to social interactions and homing. However, a large number of fishes inhabit mesopelagic and bathypelagic habitats or feed nocturnally, therefore their visual systems must cope with low light levels. While fishes in low light environments are known to use mechanoreception (Janssen, 1997; Montgomery & Macdonald, 1987), electroreception (Von Der Emde & Bleckmann, 1998) and chemoreception (Pohlmann, Grasso, & Breithaupt, 2001) to school and forage, vision may also play

an important role (Blaxter, 1980; Collin, Lloyd, & Wagner, 2000; Collin & Partridge, 1996; Holzman & Genin, 2003; Ryer & Olla, 1999; Warrant, 2004).

Many adaptations for nocturnal vision in vertebrates, including fishes, may be explained on the basis of a tradeoff between acuity and sensitivity (Lythgoe, 1979; Warrant, 2004). In general, increased sensitivity, through spatio-temporal summation of neural signals from the rods, will result in a decrease in visual acuity (Land, 2000; Lythgoe, 1979; McFarland, 1991; Warrant, 1999). Similarly, well-developed tapeta will increase photon capture, and hence increase sensitivity, at the expense of a decrease in signal to noise ratios (Warrant, 2004). Consequently, the image projected onto the fish's retina may lack details, and the fish will see a blurred image of the prey when it strikes. If, on the other hand, the projection of the image on the retina provides enough information (as in daytime), the fish may try to accommodate, so as to bring the image to maximal sharpness.

\* Corresponding author. Fax: +972 8 6374329.

E-mail address: [roi@pob.huji.ac.il](mailto:roi@pob.huji.ac.il) (R. Holzman).

In animals that strike at individual prey, accommodation can also contribute to the strike's success by providing (or improving) a measure of distance to prey. In the sandlance (*Limnichthyes fasciatus*), a small planktivorous teleost, estimation of the distance to its prey can consist of monocular vision, utilizing accommodation or parallax information generated by rotation of the eye (Pettigrew, Collin, & Fritsches, 2000). Similarly, chameleons (Harkness, 1977), horned lizards (Ott, Ostheim, & Sherbrooke, 2004) and the barn owl (Wagner & Schaeffel, 1991) were shown to use accommodation as a mean of judging the distance to their prey.

Information on accommodation under low light levels in unrestrained vertebrates is relatively uncommon, and indicates no clear pattern in the relationships between accommodative and nocturnal abilities. Thus, very few of some 15 species of Tytonidae (barn owls; Howland, Howland, Schmid, & Pettigrew, 1991), showed a marked ability of accommodation ( $>10$  D) while all others showed a limited ability of  $<2$  D (Howland et al., 1991). The nocturnally active brown kiwi showed accommodation of 7.5 D (Howland, Howland, & Schmid, 1992). In fishes, accommodation has been previously described for diurnal species during predatory strikes (e.g. Andison & Sivak, 1996; Kawamura & Kishimoto, 2002; Sivak & Howland, 1973). While morphological evidence suggest that low light fishes do accommodate (Collin & Partridge, 1996), to the best of our knowledge there are no direct observations on accommodation during prey capture in nocturnal fishes.

Apogonid fishes dominate the guild of nocturnal planktivores in Indo-Pacific coral reefs, where they are most abundant in lagoons and the leeward sections of the reef (Hobson & Chess, 1978; Marnane & Bellwood, 2002). *Apogon annularis* (Rüppell, 1829) is a small (7–10 cm) planktivorous reef fish, with relatively large eyes ( $\sim 5$  mm diameter, 47% of head length) and a moderately large mouth ( $\sim 8$  mm). Similar to other nocturnal fishes, *A. annularis* exhibits a strong selectivity for larger prey (Holzman & Genin, 2003; Holzman & Genin, 2005). Prey capture in *A. annularis* involves a rapid lunge (at  $\sim 12.8$  cm  $s^{-1}$ ) to distances of up to 4 fish body lengths, ending with opening the mouth and engulfing the prey (Holzman & Genin, 2003).

In a previous study, the rate of prey capture (adult, non-brooding *Artemia*) by *A. annularis* under controlled conditions was observed to increase from nearly zero predation at  $1 \times 10^{-6}$   $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  to  $\sim 7$  prey  $\text{min}^{-1}$  at  $4.6 \times 10^{-5}$   $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  (equivalent to  $6.022 \times 10^5 - 2.77 \times 10^7$  millions of photons  $\text{m}^{-2} \text{s}^{-1}$ ;  $1 \text{ mol} = 6.022 \times 10^{23}$  photons), and then to level off (Holzman & Genin, 2003). Showing the same pattern, reactive distances to that prey increased with increasing light intensity from  $<5$  cm at  $1 \times 10^{-6}$   $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  to 20 cm at  $4.6 \times 10^{-5}$   $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  (Holzman & Genin, 2003). Moreover, the probability of prey from different size groups to pass undetected through the fish's reactive volume corresponded to their "apparent length," as seen from the fish's perspective (see "Prey projected length"; Holzman & Genin, 2005).

These results have led to the conclusion that nocturnal predation in *A. annularis* is visually guided, or at least visually mediated. While the visual capabilities of nocturnal fishes were studied at the behavioral level by determining the light level at which feeding or schooling commence (Batty, Blaxter, & Richad, 1990; Macy, Sutherland, & Durbin, 1998; Ryer & Olla, 1999), little is known of their perceptual and physiological abilities.

Our objective in this study was to track the refractive state of the eye of *A. annularis* during prey capture under low light conditions. Photoretinoscopy (Schaeffel, Farkas, & Howland, 1987) was used to determine the relative state of accommodation while the fish were searching and striking at prey in an experimental aquarium. Anatomical measurements were then used to assess the relationships between the visual acuity and reactive distance to prey of known size.

## 2. Materials and methods

### 2.1. Experimental subjects

Four *A. annularis* individuals (average SL =  $4.65 \pm 0.55$  cm, average pupil diameter =  $3.98 \pm 0.17$  mm) were collected at the coral reef in front of the IUI marine laboratory in Eilat, using hand nets and a powerful torchlight and transported immediately into the experimental aquaria ( $30 \times 30 \times 7$  cm). Three of the walls of these aquaria were covered by black cloth, to reduce reflectance from the IR source (see below). The fish were allowed several days (at least 72 h) to acclimatize under a natural day: night cycle with running seawater at 20–22 °C. Fish were fed nightly with adult brine shrimps (*Artemia sp.*), but were deprived of food 24 h before the experiment started. This species was chosen following a screening of several species (*Apogon cookie*, *Apogon cyanosoma*, *Cheilodipterus lachneri*) due to its relatively large eyes, rapid acclimatization, readiness to feed in captivity, and the wealth of data on its feeding under low light (Holzman & Genin, 2003, 2005).

### 2.2. Measurements of the refractive state

The refractive state of the fish eye was tracked using an infrared (IR) photoretinoscope described in detail by Schaeffel et al. (1987). This system allows real-time, remote tracking of the refractive state of the eye of a fish, thus having minimal effects on the subject's behavior. In brief, the photoretinoscope is based on a light source adjacent, and eccentric to the optical axis of a video-camera lens, that projects light rays parallel to the camera's axis, which then records light reflections from the fundus. IR light (emission peak 880 nm) is used to minimize disturbance to the animals. The reflected light appears as a crescent in the pupil, and the position of the reflex indicates the position of focusing relative to the plane of the camera. In hyperopia the reflex appears at the top of the pupil (Fig. 1), whereas in myopia the reflex appears at the bottom of the pupil. The distance of focusing away from the camera plane, also termed defocus, ( $D$ ; diopters) may be obtained from the size of the reflex:

$$D = \frac{E}{2 \times A \times DF \times R} \quad (1)$$

where  $E$  is the eccentricity of the light source,  $A$  is the distance of camera to eye,  $DF$  is the dark fraction in the pupil (Fig. 1), and  $R$  is the pupil radius ( $A$ ,  $R$  and  $E$  in m). Of the five light sources located at different eccentricities (2, 6.2, 10.5, 14.5, and 18.9 mm; hereafter eccentricity levels 1–5) we used those at 6.2 and 10.5 mm, as they provided the clearest image of the pupil.

The photoretinoscope lens (Nikkor SC,  $f = 55$  mm, 1:1.2, Nikon, Japan) was positioned at 1.0 or 0.6 m from the center of an experimental aquarium facing its wide dimension ( $A$  was assumed constant at 1.0 or

Download English Version:

<https://daneshyari.com/en/article/4035778>

Download Persian Version:

<https://daneshyari.com/article/4035778>

[Daneshyari.com](https://daneshyari.com)