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A taste of the deep-sea: the roles of gustatory and tactile searching behaviour in the grenadier fish *Coryphaenoides armatus*.

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Abstract

The deep-sea grenadier fishes (*Coryphaenoides* spp.) are among the dominant predators and scavengers in the ocean basins that cover much of Earth's surface. Baited camera experiments were used to study the behaviour of these fishes. Despite the apparent advantages of rapidly consuming food, grenadiers attracted to bait spend a large proportion of their time in prolonged periods of non-feeding activity. Video analysis revealed that fish often adopted a head-down swimming attitude (mean of 21.3° between the fish and seafloor), with swimming velocity negatively related to attitude. The fish also swam around and along vertical and horizontal structures of the lander with their head immediately adjacent to the structure. We initially hypothesised that this behaviour was associated with the use of the short chin barbel in foraging. Barbel histology showed numerous taste buds in the skin, and a barbel nerve with about 20,000 axons in adult fish. A tracing experiment in one undamaged animal revealed the termination fields of the barbel neurons in the trigeminal and rhombencephalic regions, indicating both a mechanoreceptive and a gustatory role for the barbel. Our conclusion was that olfactory foraging becomes ineffective at close ranges and is followed by a search phase using tactile and gustatory sensing by the barbel. The development of this sensory method probably co-evolved alongside behavioural changes in swimming mechanics to allow postural stability at low swimming speeds.

Keywords: Fishes, Morphology, Neurophysiology, Foraging, Behaviour

Introduction

Animals living in the abyss require sophisticated means to identify, track and locate food in the absence of solar light. Using bioluminescence at several wavelengths, lateral lines and electrical field sensing, fishes are capable of hunting in continually dark habitats such as caves, turbid river water and at night (von der Emde *et al.*, 2004). Fishes are among the most conspicuous of the animals inhabiting continually dark habitats, and here a spectacular array of sensory and concealment adaptations is apparent (Herring, 2002). Even in the most oligotrophic abyssal environments an active scavenger-predator community exists. In the abyssal Atlantic (Collins *et al.*, 1999), Pacific (Priede *et al.*, 1990), and Mediterranean (Jones *et al.*, 2003) this community is dominated by small crustaceans and fishes. Amongst the fishes, it is the Actinopterygii, notably the macrourids that are most abundant, Chondrichthyes and Agnatha being largely absent from this region (Priede *et al.*, 2006). Macrouridae belong to the order Gadiformes which are characterised by the possession of one or more sub-mandibular barbels. The sensory function of barbels appears to be greater in demersal than pelagic Gadiforms (Harvey and Batty, 2002), but their role in abyssal fishes is not known.

Understanding the sensory biology of deep-sea animals is critical to understanding how they are able to maintain viable populations under severe resource restrictions. The effect of brain size and sensory orientation on the energy balance of animals is poorly understood, but catfish brain citrate synthase activity (CS, an indicator of aerobic metabolism) is 2-4 times higher (per g tissue) than muscle CS activity (Tripathi and Verma, 2004). This finding indicated that investment in sensory apparatus does have energetic consequences. *Coryphaneoides armatus* brain anatomy changes ontogenetically, with the relative volumes of the optic and olfactory areas reversing as the importance of scavenging to the fish increases (Wagner, 2003). The implication of the ontogenetic restrictions in the volumes of some brain areas is that there is an energetic benefit to reducing the volume of brain areas that become less useful as the animal's behaviour and ecology change. It is reasonable to

assume that energetic expenditure on sensory systems has been subject to powerful selective pressure, towards optimising the fishes' ability to find food and evade predators within a restricted energy budget.

Most anatomical and behavioural investigations of deep ocean scavengers have concentrated on the roles of olfaction and vision in deep sea fishes (Douglas and Partridge, 1997; Wagner, 2001; Wagner *et al.*, 1998; Wilson and Smith, 1984), and olfaction and mechanoreception in crustaceans (Klages *et al.*, 2002; Premke *et al.*, 2003). The optic system must deal with a profoundly altered visual environment in the deep sea, as the absence of solar light prevents the illumination of complex scenes. Light sources occur as intermittent bursts or patterns of bioluminescence, requiring adaptive changes at multiple stages of visual input processing (Warrant, 2000; Warrant and Locket, 2004). Catfishes that hunt in complete darkness use the lateral line system to track moving prey (Pohlmann *et al.*, 2004), while gustation is used to decide whether to strike live prey and to find dead food (Atema, 1971; Pohlmann *et al.*, 2004). Such studies involved sophisticated, controlled, laboratory experiments. Sensory experimentation in deep-water fishes is in its infancy (Widder *et al.*, 2005), as recovering these animals to the surface intact is extremely difficult (Drazen *et al.*, 2005). The major tools for understanding the senses of deep-sea fishes remain inferences from anatomical studies of captured fishes (Wagner, 2001) and *in situ* video and acoustic observations (Premke *et al.*, 2003; Wilson and Smith, 1984). The importance of olfaction has been highlighted in several scavenging deep-sea taxa (Premke *et al.*, 2003; Wagner, 2001; Wilson and Smith, 1984).

The present study simulates a small food fall, consisting of two mackerel carcasses. The carrion derived from small falls can make up a large proportion of abyssal fish stomach contents (J.C. Drazen unpublished data), even in locations where carrion is seldom observed on the seafloor (K.L. Smith Jr, personal communication). These food-falls are not often seen as they probably have a very short residence time in the deep-sea environment.

The clear implication is that scavenging animals must reach the area of food-falls and quickly identify and consume the food before it is removed by competitors. Despite the apparent urgency of the situation facing an abyssal scavenger, grenadiers are frequently observed swimming past bait, and exploring structures around the food items (Jamieson *et al.*, in press). We analysed video recordings of fish feeding at the bait, and moving in the immediate area surrounding it in order to determine the biomechanical and anatomical bases for these behaviours. In particular the importance of the commonly-observed tendency for grenadiers to swim in a head-down orientation was investigated.

Methods

Field observations of fish behaviour

Baited camera experiments were carried out using the Sprint lander (Bailey *et al.*, 2003) in the Porcupine Seabight at 4040 m (N.E. Atlantic, 44° 44.7 N, 13° 58.5 W) on the 17th March 2002. The downward-looking digital video camera was mounted facing the bait at a range of 2.8 m from the seabed, giving a field of view of 1.8 x 2.6 m. The vehicle was baited with two mackerel (*Scomber scombrus*). Recordings were made over the three hours following lander touchdown, at intervals of one minute recording, followed by two minutes “on stand-by” (lights out).

The swimming speeds and body attitudes (angle to seafloor) of five fish swimming in a straight line across the field of view of the camera were determined by digitising the position of the snout and tail of each fish in each frame. Velocity was determined from the displacement of the fish’s snout vs. time. Velocities presented are “over-ground”, i.e. not “through-water”. In order to estimate the angle between the fish and the seafloor the total fish length (0.34-0.77 m) was measured while the fish was horizontal and close to known scale references (termed the “true” length). Subsequent length measurements with the fish

at an unknown angle to the seafloor (attitude, θ) were termed the “projected” length. Attitude θ was calculated from the true and projected lengths.

$$\theta = \text{ArcCos} \frac{\text{true}}{\text{projected}}$$

Anatomical studies

Six *Coryphaenoides armatus* (total fish length 0.16-0.70 m) were obtained by a single semi-balloon otter trawl (Merrett and Marshall, 1981) haul at 3071-3181 m. Upon capture the fish were immediately placed on ice, weighed, measured and identified to species (fish parameters provided in Table 1).

1. Barbel histology. Barbels were cut at the base, fixed for several hours in a mixture of 4% paraformaldehyde and 2.5% glutaraldehyde in phosphate buffered saline (PBS, containing 3% sucrose), and stored in PBS until arrival in the home lab, where they were cut into three pieces (tip, middle, base), postfixated in 1% osmium tetroxide, and embedded in Epon. One-micron cross sections were cut off all samples and stained with methylene blue and Azur II. After identification of the remaining patches of epidermis, the blocks were reoriented and the epithelium cut parallel to the surface (tangentially).

2. Quantitative measurement of barbel axons. For a quantitative assessment of the number of axons in the barbel nerve we used sections of the basal pieces, and in case of the largest specimen also of the tip (Table 1). Using the morphometric software of the Axioplan microscope (Zeiss) we first determined the surface area of all the nerve bundles in the basal-most cross section. Next the number of axons was counted in unit areas of 300 μm^2 in 50 randomly chosen bundles. From these data the total number of axons was determined. The actual percentage of the total nerve area analysed varied between 4.2 and 46.7% (Table 1). We distinguished between myelinated and unmyelinated axons.

3. Tracing the barbel nerves. To study the projection areas in the brain, crystals of 1,1'-dioctadecyl-3,3',3',3'-tetramethylindocarbocyanine perchlorate (DiI, Molecular Probes, Eugene, OR, USA) were applied to the stump of the barbel of the smallest specimen immediately after removal of the barbel. The entire head was fixed in 4% paraformaldehyde and stored at 4°C for about two years. The brain was then isolated, photographed, and cross sections prepared in a cryostat. These were stained with hemalum and studied in a confocal microscope (CLSM 510, Zeiss) using a transmitted light channel combined with a green laser to visualise the long wave fluorescence of the transported DiI.

Results

Fish foraging behaviour

When swimming across seafloor the fish exhibited a wide range of velocities (0.02 - 0.09 m · s⁻¹, mean 0.06 m · s⁻¹) and attitudes (0 – 39°, mean 21.3°). There was a significant negative relationship between swimming speed and body angle ($r^2 = 0.31$, $p < 0.001$ $y = 47.4 - 509.6x$), see Fig. 1.

The observed changes in swimming velocity and attitude changed the caudal downthrust in a non-linear fashion. The downwards component of velocity was calculated trigonometrically, and the hydrodynamic power (W) required for this velocity was estimated (Alexander, 1999). This power was divided by velocity (m · s⁻¹) to estimate force (N). The change in attitude maximised down-thrust at a velocity of 0.06 m · s⁻¹. Above and below this velocity, the net down-thrust decreased, falling to zero at approximately 0.09 m · s⁻¹.

A second type of locomotory behaviour has recently been described by Jamieson et al. (in press) from the video recordings used in the present study. The fish swam on their sides in a circular path around vertical structures in the field of view (plastic pipes), with their head

adjacent to the structure. At times, several fish adopted this “circling” behaviour, both upstream and downstream of the bait. The fish also followed horizontal metal bars and plastic tubing. Images of this behaviour, and full details of the numbers of fish and durations involved are provided in a preceding study (Jamieson *et al.*, in press).

Barbel morphology

Coryphaenoides armatus has one chin barbel, which varied in length between 5.5 and 12 mm in the specimens studied (3-4% of body length). The barbels contained a central cartilaginous rod (Fig. 2A) anchored in the mandible, and attached to ligaments and possibly muscles (Fig. 3A). Several blood vessels of different diameters ran parallel to the skeletal element. The dominant structures, however, were numerous nerves that formed a densely packed ring around the cartilage. Roughly, there were 50-60 bundles of axons near the tip of the barbel, and up to 200 in larger specimens near the base. Unfortunately, most of the delicate epidermal epithelium containing the sensory cells was lost during trawling; only isolated patches were preserved (Fig. 2). Within the stratified epithelium, light microscopy did not allow us to distinguish different cell types such as goblet or granular cells (Whitear, 1986). In two cases it was possible to study the epithelium in tangential sections (Fig. 2B). The most striking features in this view were concentric groups of cells with a cytoplasm considerably lighter than in the surrounding epidermal cells. These groups of cells strongly resemble taste buds as described by Reutter (1978), consisting of sensory cells with a lighter cytoplasm (Fig. 2B open arrows) and darker supporting cells. Where the plane of section lay close to the basal pole of the taste bud individual myelinated axons were observed, which would belong to the afferent nerves. In the limited sample available (total area ca. 4 mm²), the density of these sensory structures was about 450 mm⁻². The number of axons leaving the barbel increased with increasing size of the specimen (Table 2). In the smallest fish (total length 155-270 mm) there were between about 3,000 and 6,000 myelinated axons, whereas in the largest specimen (total length 695 mm) the nerves contained almost 20,000 axons. The nerves also included a population of unmyelinated axons, which amounted to 1-

2% of the myelinated contingent. These may have belonged to mechanosensory or nociceptive afferents.

Tracing experiments

Experiments tracing the barbel neurons' termination fields in the brain were used to corroborate the evidence for sensory modality provided by the microanatomy of the sensory structures in the barbel epithelium. Unfortunately most specimens were not in sufficiently good condition to perform these studies. In the smallest specimen, we applied a fluorescent tracer (DiI) to the base of the barbel (Fig. 3A) and studied the spread of the dye to the nerve's target areas in the brain. At the gross anatomical level, a single bright spot is observed in the posterior rhombencephalic area corresponding to the gustatory field with a small facial lobe (Fig. 3B, C, arrow). Cross sections of the isolated brain revealed two additional points of interest. Firstly, the descending portion of the trigeminal root was labelled (Fig. 4A) indicating that the barbel nerve also carried mechanosensory or nociceptive information. Secondly, the label applied to the barbel nerve appeared unilaterally in the brain.

Discussion

Abyssal grenadiers often adopt a head-down swimming orientation when foraging, the reason for which was initially unclear. A further puzzling observation was the fish's tendency to swim on their sides, moving in circles around the vertical poles of the lander structure (Jamieson *et al.*, in press). Our initial hypothesis was that the purpose of both this behaviour and head-down foraging was to allow contact between the fish's barbel and the seafloor or other structures. A test of this hypothesis was to determine whether the barbel had any sensory capability. Histological investigation of the barbel structure, and tracing of the neurological connections between the barbel and brain, appeared to confirm a sensory role for the barbel. Head-down swimming is therefore likely related to the use of barbel senses.

Body orientation in foraging fishes

Changing body orientation (tilting) in gadiform fishes is a well-studied phenomenon, as the posture of the fish affects acoustic target strength, an essential parameter in fisheries stock surveys (Hjellvik *et al.*, 2004). One behavioural role of tilting in fishes is the maintenance of stability, especially at low velocities when flow over control surfaces such as pectoral fins is reduced (Webb, 2002). Grenadiers appear to be limited to low velocities for energetic reasons (Collins *et al.*, 1999; Ruxton and Bailey, 2005) and therefore probably require active stabilisation using caudal thrust over much of their performance envelope. Many fishes are not absolutely neutrally buoyant, and/or their centre of buoyancy is ventral to their centre of mass (Webb, 2002). If the grenadiers recorded here are slightly positively buoyant or anatomically unstable, they would rely on a downward thrust component to maintain posture and proximity to the seafloor. Unfortunately, no accurate buoyancy measurements exist for abyssal grenadiers, as their gas bladders rupture upon decompression. At lower speeds a progressively higher angle would be required in order to maintain adequate down-thrust. The observed changes in angle do appear to be consistent with the maintenance of a small caudal down-thrust over the range of velocities used by *C. armatus*.

While a locomotory explanation may be possible for head-down swimming across the seafloor it cannot account for the rotational swimming observed around vertical structures. The most likely explanation here remains the use of a chemical or electrical sensory system that requires close contact between the ventral portion of the head/posterior body and a surface under investigation. The use of electroreception does not appear likely, as this detection method is not known in any other members of the Gadidae. Likely chemical sensing structures are the chin barbel and fins (Kotrschal and Whitear, 1988; Kotrschal *et al.*, 1993). Unfortunately the fins were severely damaged during trawl recovery and could not be studied. Our video observations did not include any apparent fin contact with the

structures or the bottom, and in all cases the chin barbel was the most likely point of contact. Entrainment of the odour plume around the lander structures, resulting in an olfactory search of the structure is also possible. At various times different fish were observed following structures both up- and down-stream of the bait, and so it appears that it was the structure being examined, rather than the water around it.

What is the role of the barbel?

Whatever the cause of head-down orientation and rotational swimming around objects, the effect is to place the ventral portion of the head and the small chin barbel in contact with the surface. The barbels of these grenadiers are short (12 mm in a 695 mm fish), and would not reach the seafloor if the fish were horizontal. The morphology of the barbels has probably co-evolved with the swimming behaviour of the fish, but it is only when the fish's foraging behaviour was observed that the possible importance of the barbel became apparent.

Histological analysis of the barbel itself and tracing of the afferent axons from the barbel indicate both a gustatory and mechanosensitive role for the barbel, though the tracing experiment in a single individual must be interpreted with caution. We suggest that the barbel is only used when in contact with the seafloor or other surfaces. Termination of some of the barbel neurons in the trigeminal area of the brain suggests that the barbel also has a mechanosensory role; this supports the suggestion that the barbel is used while in contact with surfaces. The single-sided termination of the barbel nerves is an interesting, but unexplained finding. As mentioned previously, this finding is based on a single tracing experiment, and further experiments in this and related species would be required to ascertain the prevalence and importance of this unilateral termination.

Barbels have been widely studied, especially in catfishes, where they are used to detect food in low-visibility environments. In all previous examinations of fish barbels the barbel tastebuds are neurally connected to cranial nerve VII, and in some species trigeminal tactile

sensory fibres have also been observed (Fox, 1999). From the small amount of data available in this study it appears that these grenadiers have around 450 mm⁻² taste buds in the barbel skin, which is in the same range as in cod and other shallow-water gadids (Harvey and Batty, 2002). The level of taste system development in fishes has previously been linked to the degree of benthic association of the fish, and the light level and water clarity of its habitat (Fishelson and Delarea, 2004; Franz-Odenaal and Hall, 2006; Harvey and Batty, 2002). *Coryphaenoides armatus* has barbel taste bud densities similar to ecologically similar fish in the relatively well-lit surface waters, giving no evidence for the sort of increased taste sensitivity seen in comparative studies between light- and dark-living cave fish populations (Franz-Odenaal and Hall, 2006). It may be that light (as bioluminescence) continues to be of ecological relevance to *C. armatus* (which have large eyes), in a way that it is not for cave fishes and those living in very turbid water.

We propose that head-down foraging is a close-range search mechanism used to determine the exact location of food items, and potentially to map out the fish's local environment. It is possible that the information provided by odour concentration is not sufficient to allow the final stage of searching, and that the animal simply responds to odour above a threshold by rheotaxis. Once the animal is close to the odour source it is possible that this signal will become ineffective and a tactile and gustatory search must begin. In addition to determining the exact location of food, the barbel likely serves to examine the mechanical properties of the surface of the object of interest and also to test the composition of tastants emanating from it. Based on these stimuli, a first decision will be taken whether to ingest the object. The barbel nerve carries only a fraction of the gustatory information. Additional taste buds are often found in the skin of the head, the fins, and in the oropharyngeal cavity of other fishes (Finger *et al.*, 2000). These latter taste buds probably determine whether the object is swallowed or discarded (Valenticic, 2004). Unfortunately, however, no details on their density and distribution are yet available in *C. armatus*.

The relative importance of the sensory input from the barbel can be inferred from the anatomy of the brain of the fish. Volumetric analyses of sensory brain areas have shown that olfaction is the most important modality for adult specimens of *C. armatus* (Wagner, 2003). The sensory orientation of the largest fish used here can be inferred from preliminary counts of the axons in the olfactory tract showing roughly 260,000 axons, compared to about 50,000 axons in the optic nerve (Wagner, unpublished) and about 20,000 axons in the barbel nerve. Ontogenetic changes in brain anatomy appear to be associated with changes in foraging strategy and prey type, away from small benthic and infaunal prey and increasing their reliance on carrion (Wagner, 2003 and J.C. Drazen pers. comm.). The comparison of axon numbers in *C. armatus* of different sizes showed an isometric increase in the number of axons at the base of the barbel with size (Table 2). This is consistent with Wagner's (2003) finding that regardless of body size the gustatory areas of the *C. armatus* brain occupied the same proportion of the brain volume. Previous reports on the gustatory system of catfishes also demonstrate a developmental increase in both the number and diameter of the myelinated and unmyelinated neurons serving taste buds (Finger *et al.*, 1991). Unfortunately we have insufficient data to know whether *C. armatus* also show catfish-like patterns of scaling in the abundance of taste buds.

Conclusions

The abyssal grenadiers studied here used head-down orientation when swimming, probably because swimming at low speeds causes difficulties in maintaining postural stability. This behaviour also allows the chin barbel to contact the seafloor while the fish is swimming forward, and we suggest that the sensory function of the barbel has co-evolved with this behaviour. We hypothesise that gustation and mechanoreception are used by grenadiers to locate food sources once the general location has been determined by olfaction.

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Table 1: Data on barbel nerve counts for each of the fish analysed. Two samples were taken from the largest fish (15062-45). The size range is similar to the size range of the fish observed in the video recordings.

ID	sex	Size (total length, mm)	Total area of nerve (μm^2)	Percentage of		
				nerve area analysed	Unmyelinated axons	Myelinated axons
15062-36	0	155	36×10^3	47	62	35×10^2
15062-35	0	185	44×10^3	32	41	33×10^2
15062-16	M	241	53×10^3	32	47	39×10^2
15062-17	0	256	51×10^3	36	56	29×10^2
15062-14	M	270	79×10^3	17	135	64×10^2
15062-45a	F	695, base	62×10^4	4	404	19×10^3
15062-45b	F	695, tip	30×10^3	9	228	12×10^3

Table 2. Scaling of barbel axon numbers and ratio of myelinated to unmyelinated axons, with fish body length. Regression analyses with respect to pre-anal fin length (PAFL).

Parameter	Mean	SE	Scaling relationships with PAFL (m)				
			r^2	F_4	p	Intercept	slope
Total axons	14×10^4	23×10^4	0.95	72.5	0.001	85×10^5	1.97
Unmyelinated axons	12×10^1	58	0.79	15.0	0.02	29×10^2	1.49
Myelinated axons	66×10^2	26×10^2	0.84	20.8	0.10	99×10^3	1.25
Myelinated/unmyelinated	62	6.8	0.24	1.2	0.33	34	-0.24

Figure legends

Fig. 1. Relationship between swimming speed, fish attitude and caudal down-thrust from video sequences of swimming in five grenadier fish *Coryphaenoides armatus* at 4040 m in the N.E. Atlantic. Solid symbols – Attitude, Open symbols – calculated down-thrust.

Fig. 2. Microscopic anatomy of the barbel of *Coryphaenoides armatus* in 1 μm plastic sections stained with methylene blue and Azur II. A. A cross section near the tip of the barbel shows that the core of the barbel contains a cartilaginous rod (C) surrounded by several blood vessels (BV) and bundles of axons (N), which are embedded in a matrix of connective tissue. This structure is enclosed by a basal membrane (BM). Only isolated patches of epidermal epithelium (E) including 2 taste buds (TB) are conserved. B. The tangential section of an epidermal patch passes through different layers, more basal in the middle, and more superficial at the upper and lower margin. Embedded in the homogeneous population of epithelial cells are circular clusters of specialised cells with lighter staining cytoplasm, strongly resembling taste buds. Sensory cells with lighter cytoplasm (open arrows) can be distinguished from darker supporting cells. Occasionally, an axon contacting a taste bud is found (arrow)

Fig. 3. Tracing the barbel nerve with DiI in *Coryphaenoides armatus*

A. Crystals of DiI (red) were applied to the stump of the barbel (large arrow), but have been removed along with the epidermis in this preparation. The barbel nerve is indicated by the small arrow. In a laterodorsal (B) and dorsal (C) view of the brain an intense spot of DiI appears in the gustatory area of the facial lobe (arrow). Cb cerebellum; m muscle fibres; O otolith; OT optic tectum; RV rhombencephalic ventricle; V / VII trigeminal and facial nerves; VIII octavolateral nerve

Fig. 4. Histological cross sections of the *Coryphaenoides armatus* brain show the distribution of DiI label in the target areas of the barbel nerve. A) In the anterior

rhombencephalic area, shortly caudal of the entry of the trigeminal nerve (V), DiI fluorescence is seen in the area of the descending root of the trigeminal nerve (DV). **B)** More posterior, DiI fluorescence is concentrated in the area of the sensory nucleus of the facial nerve (N VII s) and the facial lobe (L VII). RV rhombencephalic ventricle. These areas indicate that the barbel nerve carries mechanosensory (trigeminal) as well as gustatory (facial) afferents.

Figures

Fig. 1.

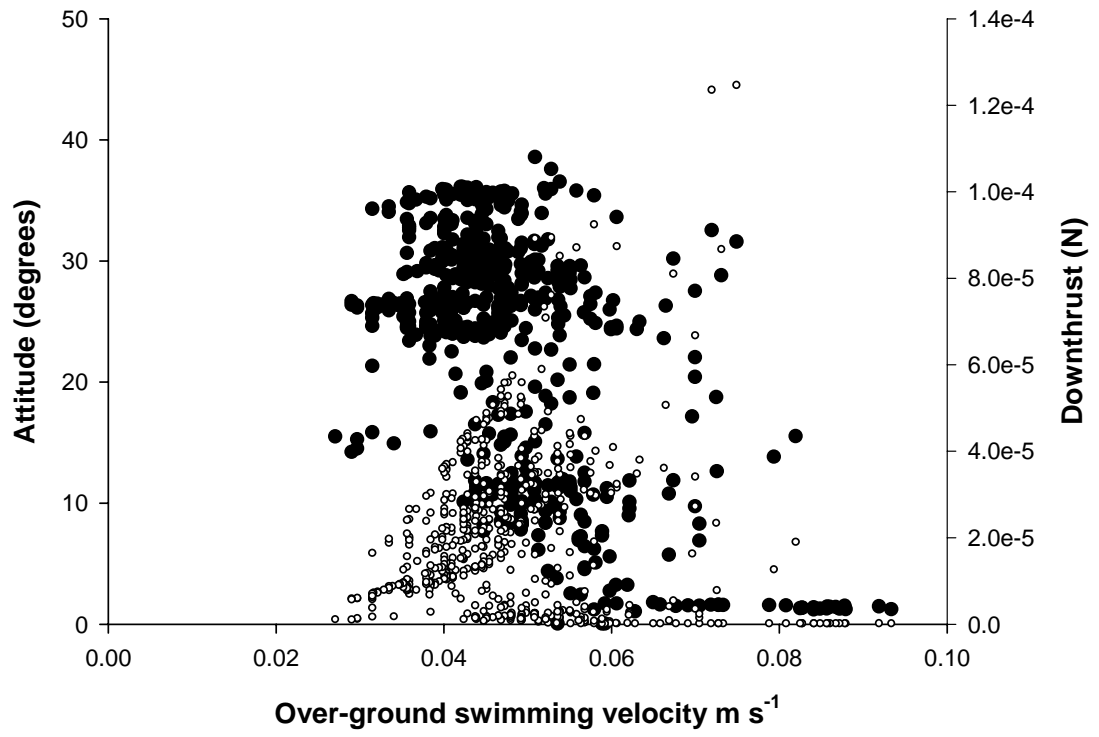


Fig. 2.

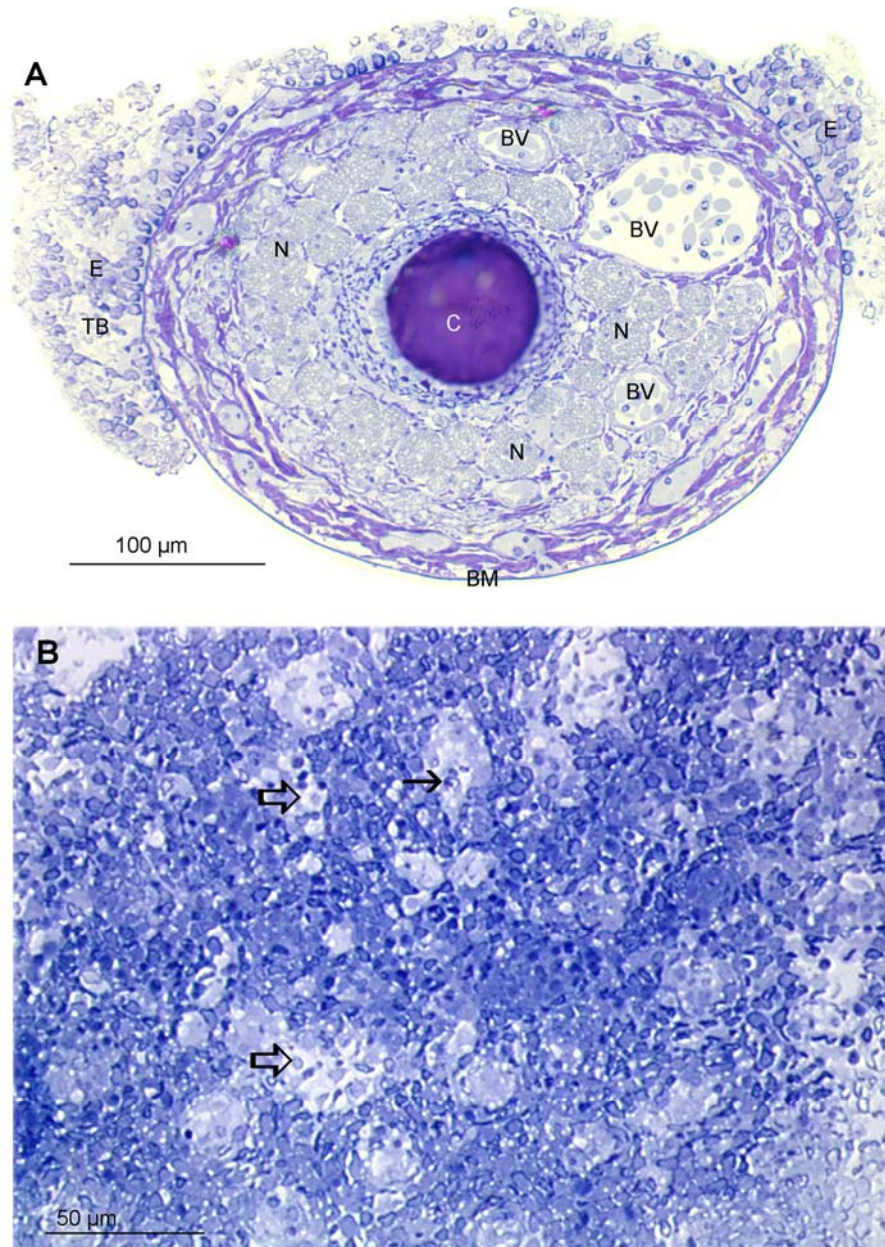


Fig. 3.

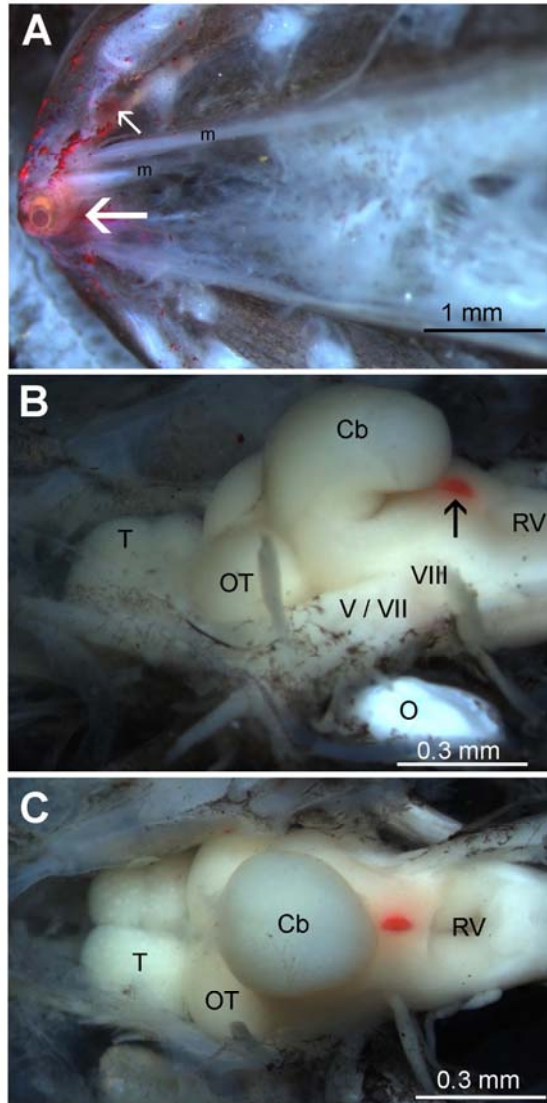


Fig. 4.

