Burrowing in fishes: anatomy, physiology, function and ecology

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Key points

- Burrowing has evolved convergently in many fish species.
- Burrowing provides escape from predation and burrows may be semi-permanent structures used throughout the life of a fish.
- Due to limitations in dissolved oxygen, burrowing fishes show behavioral and physiological adaptations allowing them to survive in hypoxic conditions.
- Soil penetration requires functional and anatomical adaptations that may differ depending on whether mouth excavation, head-first, or tail-first burrowing is used.
- Although subsurface locomotion remains poorly understood, undulatory swimming-like kinematics are observed, yet these differ between initial substrate penetration and subsurface locomotion, suggesting different underlying motor patterns and neural circuits.

Abstract

Burrowing is a ubiquitous behavior in vertebrates allowing animals to escape predators and gain access to novel resources in a relatively competitor-free environment. However, burrowing also imposes strong constraints. For example, as oxygen is limited in the sediment and in burrows, fish show specific anatomical, behavioral and physiological adaptations allowing them to survive in hypoxic conditions. In contrast to most other vertebrates, fish perform both head-first and tail-first burrowing. As most soils consist of granular media that differ in grain size and degree of compaction relatively large forces are needed to penetrate the substrate, especially for larger grain sizes. Concurrently, several anatomical adaptations, including body elongation, a fusiform head shape and a reinforcement of the head or tail, allow better substrate penetration and burrow formation. In loose soils burrowing fishes use sand-swimming behaviors that resemble typical swimming, yet that differ in the underlying kinematics and motor control. The paucity of data on burrowing in fish in contrast to the diversity of species and behaviors used by fishes makes this a rich topic for further study.

Teaching slide

See the submitted figure providing an overview of fish burrowing.

Fishes are unique among vertebrates in showing both tail-first and head-first burrowing. They show a remarkable level of convergence in their adaptations to a life underground including physiological adaptations to hypoxia. To move below the substrate some fishes use modified undulatory kinematics. Fish drawings were inspired by the following pictures: *Heteroconger*: Smithsonian National Museum of Natural History (link: http://n2t.net/ark:/65665/m3ad69548c-248a-4f95-b72c-45a6418b6fcd); *Pisodonophis*: Fishes of Australia, Dinh D. Tran, FiMSeA (link: http://ffish.asia).

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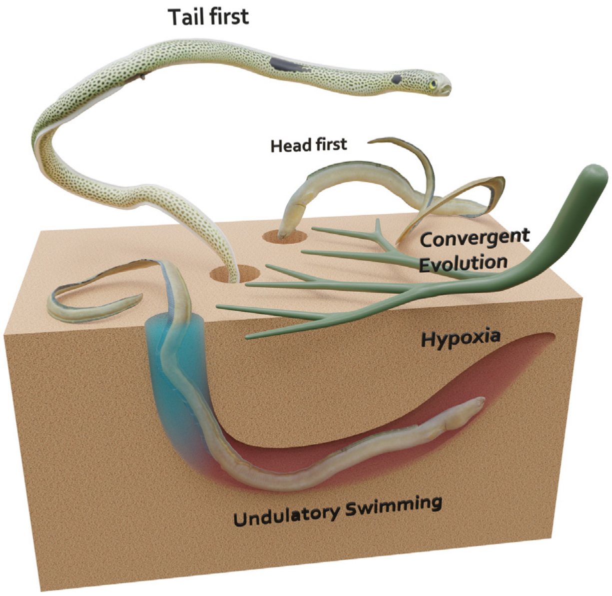

Introduction

Burrowing has fascinated scientists for nearly two centuries (Osler, 1826). It is an unusual life-style that provides several advantages, such as access to a relative predator-free environment, novel resources, and a stable environment. However, to invade this novel niche animals must overcome several constraints that shape the morphology and physiology of these species (Dorgan et al., 2006). These constraints are often intense and lead to strong evolutionary convergences within and among major groups of vertebrates (Ebel et al., 2020; Evans et al., 2022; Le Guilloux et al., 2020; Gomes-Rodrigues et al., in press; Kraus et al., 2022). Soil and sediments (whether wet or dry) are heterogeneous, dense and often granular media, resulting in a high energetic cost of burrowing (Vleck, 1979; Navas et al., 2004). To be able to penetrate into this substrate animals show adaptations of their locomotor system, including changes in vertebral anatomy and limb morphology (Wake, 1993; Lowie et al., 2022). Moreover, many burrowing vertebrates are elongate head-first burrowers that have to resist the forces imposed onto the cranium during soil penetration (Wake, 1993). Given that the head also houses the brain and the sensory organs, these head-first burrowers often show robust and highly fused cranial bones (Kearney and Stuart, 2004; De Schepper et al., 2005). However, fishes stand apart from most other vertebrates in having specialized tail-first burrowers resulting in unique adaptations of the caudal area (De Schepper et al., 2007a,b). In addition to the physical constraints imposed by the medium, the underground environment also imposes additional constraints including a low oxygen concentration (McNabb, 1966). These have resulted in both physiological and behavioral adaptations in many burrowing vertebrates, including fish. Surprisingly, and despite the ubiquitous nature of burrowing in fishes (Liem, 1967; Minckley and Klaassen, 1969; Berra and Allen, 1989; De Schepper et al., 2005; Dunn and O'Brien, 2006; Evans et al., 2022) relatively few studies have explored the many ways that fish have become adapted to such a burrowing life style. In the following paragraphs we review the ecological and behavioral, anatomical, physiological and locomotor specializations that have been described in burrowing fishes.

Ecology and behavior

Given the diversity of substrates in which fish burrow, an equally great diversity in burrowing styles and burrow types can be observed. Fish typically either use mouth excavation (Rice and Johnstone, 1972; Colin, 1973; Atkinson and Pullin, 1996), head-first burrowing (De Graeve, 1970; Atkinson et al., 1987; Bilecenoglu, 2005; De Schepper et al., 2005), tail first burrowing (De Schepper et al., 2007a,b), or a combination of these to penetrate the substrate and create more or less permanent burrows. Burrowing has been suggested to be an anti-predatory behavior in many fishes providing them with a refuge from predators (De Graeve, 1970; Kawamura et al., 1975; Glodek and Voris, 1982; Nemtzov, 1994; Bilecenoglu, 2005) or allowing them to escape unfavorable climatic conditions such as droughts (Carlson, 1968; Berra and Allen, 1989; Liem, 1967). Burrows can be semi-permanent to permanent (Colin, 1973; Nash, 1980) depending on the substrate and often leave permanent marks in the fossil record (Carlson, 1968; Benton, 1988). In loose, sandy substrates fish can burrow using sand-swimming behaviors (Gidmark et al., 2011; Bizzarro et al., 2016), superficially similar to those observed in other vertebrates (Pagett et al., 1998; Baumgartner et al., 2008; Jung, 2010). The burrows made by fish vary in shape and size and can range from simple vertical burrows terminating into an expanded chamber (Colin, 1973; Atkinson and Pullin, 1996) to burrows that are more complex and contain multiple openings (Rice and Johnstone, 1972; Nash, 1980; Atkinson and Pullin, 1996). These additional openings may serve as ventilation shafts (Atkinson et al., 1987) or provide additional escape routes from the burrow. Some fishes have been observed to actively irrigate the burrows, presumably to maintain adequate oxygen levels (Pullin et al., 1980; Atkinson et al., 1987). Burrow size is dependent on fish size in most species studied with the diameter of the burrow generally corresponding to the diameter of the fish (Atkinson and Pullin, 1996). Burrow construction in captivity ranges anywhere from several hours to several days, depending on the size of the fish and the type of substrate (Rice and Johnstone, 1972; Colin, 1973; Atkins and Pullin, 1996). The burrows of fish have been suggested to play an important role in bioturbation with a redistribution of coarser material toward the surface (Atkinson and Pullin, 1996). Interestingly in many species, burrows intersect burrows of other species resulting in interspecific associations (Atkinson and Pullin, 1996). Alternatively, some fishes use burrows from other organisms and do not actively create their own burrows (Rice and Johnstone, 1972).

Anatomy

Surprisingly few comparative studies of burrowing adaptations exist. However, a recent study showed that burrowing wrasses typically possess elongated and narrow bodies with streamlined, pointed heads (Tatom-Necker and Westneat, 2018). Moreover, robust prezygapophyses and long neural spines were observed in these sand-diving wrasses. It has been suggested that this may provide greater stiffness (Tatom-Necker and Westneat, 2018) while likely also providing an increase in the insertion area of the anterior epaxial muscles used to generate the forces needed to penetrate the substrate. A further comparative phylogenetically-informed study using 3D geometric morphometric approaches found that burrowing evolved at least twice independently in wrasses. Moreover, burrowing wrasses exhibited overall narrower heads compared to non-burrowing wrasses, despite showing a great diversity in shape (Evans et al., 2022). The authors further showed that despite showing similar degrees of morphological disparity, burrowing wrasses took more time to arrive at that level of disparity compared to non-burrowing wrasses (Evans et al., 2022).

A unique feature of burrowing fishes in comparison to other vertebrates is that some species have evolved a specialized in tail-first burrowing behavior (De Schepper et al., 2007a,b). Garden eels (*Heteroconger*) are undoubtedly one of the best-known examples, and anatomical investigations have shown that the caudal skeleton in these tail-first burrowers is reduced and more robust in comparison to other eels (De Schepper et al., 2007a). Moreover, the intrinsic caudal muscles are reduced or even absent (De Schepper et al., 2007a). Interestingly, and in contrast to head-first burrowers (Bozzano, 2003), the eyes in these tail-first burrowers are well developed. In head-first burrowing eels the eyes are reduced, the cranial lateral line system is modified and the overall head shape is fusiform (De Schepper et al., 2005). Several head-first burrowers have hypertrophied jaw muscles and these have been suggested to play an important role in preventing the disarticulation of the protruding lower jaw during head-first burrowing (De Schepper et al., 2005; Gidmark et al., 2011). These species typically do not use mouth excavation but rather push their head into the substrate using shoveling movements (Steendam et al., 2020). In *Moringua edwardsi*, the skull is hyperossified, resulting in the fusion of several cranial bones and the presence of scarf joints with large overlapping areas (De Schepper et al., 2005). This is presumed to be important to resist the forces imposed upon the skull during burrowing as suggested for other vertebrates (Gans, 1974). Indeed, finite element models suggest that the skull in the head-first burrowers is indeed better suited at resisting forces induced by burrowing compared to tail-first burrowers (Herrel et al., 2011a). Interestingly, some species such as the rice paddy eel (*Pisodonophis boro*) use both head-first and tail-first burrowing behaviors (De Schepper et al., 2007b). This species shows reduced eyes covered by thick corneas that may protect the eyes during burrowing, an elongate and pointed skull, and robust cranial bones and joints. On the other hand, this species also has a pointed tail and a consolidated caudal skeleton with reduced caudal muscles, thus combining adaptations for both burrowing modes (De Schepper et al., 2007b).

Overall, the literature suggests that head-first burrowing imposes strong constraints leading to specific morphologies facilitating substrate penetration. Beyond the changes in overall head shape other morphological adaptations can be expected to occur in burrowers. For example, many burrowing fishes live in low-light conditions and are nocturnal. In the rufus snake eel, *Ophichthus rufus*, the visual system shows specializations allowing it to identify the mouth of its burrows (Bozzano, 2003). In addition, the retina in this species was strongly vascularized, a possible adaptation to the hypoxic conditions in the burrow (Bozzano, 2003). Similarly, strong vascularization of the central nervous system has been observed in mud-burrowing gobids, suggesting that an increased vascularization of the brain and sensory organs may be an important adaptation to life in hypoxic conditions present in burrows (Kenchington and Choy, 1989). Yet, whether these observations can be generalized to other taxa remains to be tested. Finally, several studies have also shown the presence of smooth skin and numerous mucous glands in the skin providing lubrication during burrowing as well as preventing desiccation in some species (Liem, 1967).

Physiology

Despite the advantages of burrowing in providing a stable and safe environment, it also provides fish with an extreme environment that is both hypoxic (low O_2 concentrations) and hypercapnic (high CO_2 concentrations, up to five times that of normal sea water; Atkinson et al., 1987). Several studies have measured the oxygen consumption rate in burrowing fishes and have found low critical oxygen tension in burrowing species (Pullin et al., 1980; Atkinson et al., 1987; Pelster et al., 1988a; Quinn and Schneider, 1991). Some species also show high anaerobic capacity allowing a switch to an anaerobic metabolism when the environmental oxygen concentration is too low (Pelster et al., 1988a). However, such an anaerobic metabolism can only be maintained for short periods of time (Pelster et al., 1988a,b). Consequently, most species have been observed to irrigate their burrows to maintain PO_2 levels that correspond to the critical oxygen tension for oxygen consumption (Pullin et al., 1980; Atkinson et al., 1987) and reconstruct burrows rapidly if they collapse causing anoxic conditions (Pelster et al., 1988a). In several species the blood showed a marked Bohr effect and low buffering capacity (Bridges et al., 1982; Pelster et al., 1988b). The Bohr effect describes the oxygen-binding affinity of hemoglobin in relation to the concentration of carbon dioxide. As the blood pH decreases through hyperventilation in response to low oxygen conditions, the hemoglobin dissociation curve shifts to the left increasing the oxygen affinity of the hemoglobin (Bridges et al., 1982). Overall, however, physiological adaptations to hypoxia appear limited and ventilation of burrows seems an essential behavioral strategy allowing these fish to survive.

Locomotion

Only few studies have quantified the kinematics and mechanics of soil penetration in burrowing fish. The least specialized species that live in loose granular substrates use what is referred to as sand-swimming (Gidmark et al., 2011; Bizzarro et al., 2016). However, the mechanics of underground locomotion and substrate penetration are highly dependent on the substrate (Herrel and Measey, 2010). For example, laboratory measurements of penetration forces using 3D-printed heads of sand lances, *Ammodytes personatus*, show that there is a non-linear relationship between penetration force and grain size with coarser sediments being much more difficult to penetrate (Bourdillon, 2011). Interestingly, in nature this species prefers coarse sand suggesting that substrate selection is not purely driven by the mechanics or energetic cost of substrate penetration (Bizzarro et al., 2016). Indeed, coarser grained sediments may provide less hypoxic conditions providing an advantage. *In vivo* observations of substrate penetration and subsurface using X-ray or regular high-speed video have been performed for only a handful of species: the sand lance (Gidmark et al., 2011), the European eel (*Anguilla anguilla*; Steendam et al., 2020), the rice paddy eel (Herrel et al., 2011a,b), and the slippery dick wrasse (*Halichoeres bivittatus*; Tatom-Necker and Westneat, 2018). These studies all show that burrowing consists of a two-stage behavior (sometimes three) characterized by a first step of substrate penetration using typical undulatory swimming motions. Next, a subsurface locomotion phase is observed that differs significantly in its kinematics and typically involves high-amplitude, low-frequency waves. This is reminiscent of what has been documented for burrowing in larval lamprey (Pagett et al., 1998; Katz et al., 2020). Based on electromyographical recordings of the body muscles during burrowing the authors suggested that in lamprey the motor pattern and underlying neuronal circuits responsible for the initial substrate penetration are identical to those observed during swimming, yet the motor patterns for subsurface locomotion were significantly different (Pagett et al., 1998). Interestingly, the subsurface component of burrowing locomotion can be characterized either by a very high slip factor indicating a transition to non-slip wave locomotion (Gidmark et al., 2011; Herrel et al., 2011a,b). This suggests that the substrate behaves more like a solid in these burrowing fishes in contrast to terrestrial sand swimmers where the sand appears to be fluidized (Maladen et al., 2009).

Conclusion

In contrast to what has been suggested in the literature, burrowing is rather common in fishes and has been observed in a wide variety of groups. Burrows can be complex and burrow structure varies in function of fish size and substrate characteristics. Burrows can be occupied during the entire life of an animal and provide escape from predators. Burrowing can take place through mouth excavation, head-first, or tail-first burrowing. Fish show adaptations to these different behaviors and often the part of the body penetrating the substrate first is strengthened. The overall shape of burrowing fishes is generally elongate with narrow and streamlined heads facilitating substrate penetration in head-first burrowers. Physiological and behavioral adaptations to the low oxygen concentrations in the burrows are present and involve burrow irrigation and flexibility in the oxygen affinity of the hemoglobin due to a large Bohr effect. Subsurface locomotion differs significantly from initial substrate penetration and swimming and is likely governed by a different motor pattern. Given the amazing diversity in shapes and forms that can be observed in burrowing fishes and the low number of species studied to date, studying the adaptations to this unique way of life is a very fruitful avenue for further research.

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