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REVIEW

Patterns and processes in amphibious fish: biomechanics and neural control of fish terrestrial locomotion

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ABSTRACT

Amphibiousness in fishes spans the actinopterygian tree from the earliest to the most recently derived species. The land environment requires locomotor force production different from that in water, and a diversity of locomotor modes have evolved across the actinopterygian tree. To compare locomotor mode between species, we mapped biomechanical traits on an established amphibious fish phylogeny. Although the diversity of fish that can move over land is large, we noted several patterns, including the rarity of morphological and locomotor specialization, correlations between body shape and locomotor mode, and an overall tendency for amphibious fish to be small. We suggest two idealized empirical metrics to consider when gauging terrestrial 'success' in fishes and discuss patterns of terrestriality in fishes considering biomechanical scaling, physical consequences of shape, and tissue plasticity. Finally, we suggest four ways in which neural control could change in response to a novel environment, highlighting the importance and challenges of deciphering when these control mechanisms are used. We aim to provide an overview of the diversity of successful amphibious locomotion strategies and suggest several frameworks that can guide the study of amphibious fish and their locomotion.

KEY WORDS: Amphibious fishes, Biomechanics, Fish walking

Introduction

Amphibious fishes are a large and diverse group of animals, overcoming many physiological challenges across the water and land environments (Damsgaard et al., 2020; Graham, 1997; Wright and Turko, 2016). These fish must change their biomechanical performance to accommodate the terrestrial environment, and have done so in a variety of ways using a diversity of body shapes and sizes (Table 1) (Gibb et al., 2013; Pace and Gibb, 2011, 2014; Rabosky et al., 2013). Understanding how fish locomote on land provides insight for evolutionary biologists describing the motion of the first terrestrial vertebrates (Clack, 2002), inspiration for engineers when designing versatile robots (McInroe et al., 2016; Ren and Yu, 2021) and models for physiologists to understand the plasticity and function of physiological systems (Wright and Turko, 2016). This Review discusses the major biomechanical challenges faced when moving from water to land, and, briefly, the consequences of these environmental changes on the biological tissues and behaviour of fishes. It builds on a recently proposed scoring system that combines land use and emersion tolerance to determine the 'amphibiousness' of fishes (Turko et al., 2021) and, specifically, expands this approach for scoring land use

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by integrating biomechanical measures of terrestrial locomotion. We also include a brief discussion of what constitutes 'terrestrial locomotion' in fishes with a description of 'effective performance' and 'effective distance' as two idealized empirical metrics to consider when gauging terrestrial 'success'. We use a range of existing variables from the literature, grouped to support the suggested idealized empirical metrics, and explore these variables using an established phylogeny of amphibious fishes (https://fishtreeoflife.org/downloads/). We use this phylogeny to discuss what might drive the patterns of biomechanical diversity and performance we see across amphibious fishes. Finally, we discuss how neural control may constrain or enable novel modes of locomotion.

Physical constraints of land versus water

To appreciate the biomechanical challenges faced by amphibious animals, one must consider the differences in the physical environments of water and land. The density of water is almost three orders of magnitude greater than that of air, and water is roughly 60 times more viscous, which dramatically changes the physical forces experienced by an organism in motion. In water, fish body mass is supported by buoyant forces and, depending on the size of the animal, locomotion is affected by both form drag (see Glossary; owing to body shape) and frictional drag (see Glossary; owing to fluid viscosity). On land, animals must overcome gravity to reduce frictional drag against the ground, whereas form drag is functionally non-existent because the density of air is so much lower than that of water. These differences in the physical force environment change the magnitude and rate of forces experienced by the body and fins of amphibious fish, influencing the kinematics and neural control of their movements and driving plastic responses of musculoskeletal tissues supporting the body (Figs 1 and 2).

The terrestrial force environment affects fish tissue and biomechanical performance at different time scales, as illustrated by the grey bichir (*Polypterus senegalus*). After a single walking event, the fin muscle membranes in *P. senegalus* show damage in fish unaccustomed to terrestrial locomotion (Dhuper, 2018). However, on a longer time scale, prolonged exposure (weeks to months) to terrestrial environments leads to changes in muscle fiber type and bone morphology in the fin (Fig. 2) (Du and Standen, 2017, 2020; Standen et al., 2014). Thus, forces that cause damage in the short term may be important triggers for longer-term plastic responses that impact animal performance (see 'What drives effective terrestrial locomotion?' for further discussion of plasticity; Du et al., 2013; Du and Standen, 2017, 2020; Rossi et al., 2018; Standen et al., 2014; Turko et al., 2012, 2017; Wund et al., 2008). Finally, over many generations, adaptive selection may act on newly expressed phenotypes, fixing them in the genotype and helping to explain how various evolutionary transitions, such as the fin-to-limb transition, may have transpired (Clack, 2009; Moczek et al., 2011; Pfennig et al., 2006, 2010; Shubin et al., 2006). In

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Glossary

Centre of buoyancy
The position where the upward, buoyant force acts in a volume of water displaced by a mass.

Centre of mass
The average position of all of an animal's body parts, weighted according to their mass.

Dynamic loading
Loading of bones, muscles and tissues during movement.

Exaptive
Evolved as a result of natural selection for one function, but is potentially helpful in another function.

Fast-twitch muscle fibres
Muscle fibres expressing a myosin isoform capable of fast contractions. Generally anaerobic, capable of high force production and susceptible to fatigue.

Form drag
Also known as profile drag, this depends on the shape of the animal, and it results from a separation between surface and boundary layer and the wake that results from that separation.

Friction drag
Aquatic: Drag resulting from the friction of a fluid against the surface of an object moving through it. This increases with increases in viscosity. Terrestrial: Drag resulting from body or appendage contact with the ground. This can be a negative force that must be overcome to move forward, or a positive force that reduces slip during thrust production.

Fusiform
In fishes, a particular body shape that tapers at both ends, such as in streamlined fish like tuna.

Ground reaction force
The force exerted by the ground on a body in contact with it.

Locomotor mode
A distinctive movement pattern with a particular set of propulsive elements. For example, swimming, walking and jumping would be three separate locomotor modes.

Phylogenetic inertia
The limitations imposed by previous adaptations on future evolutionary pathways.

Resorbing
During bone remodelling, the reduction of bone size through a variety of processes.

Slow-twitch muscle fibres
Muscle fibres expressing a myosin isoform capable of a slower rate of cycling at moderate force outputs, but not susceptible to fatigue. These fibers usually operate aerobically.

Static loading
Loading of bones, muscles and tissues that occurs when stationary.

Trade-off
When getting better at a particular process/function occurs only at the expense of another.

addition, motor control patterns may be coopted from aquatic modes of locomotion, or they may be developed *de novo* in animals that move onto land. How the changed force environment impacts sensory feedback systems and ultimate motor control is relatively unknown but can be hypothesized to occur in a variety of ways (see 'Neural control in a terrestrial environment').

What to consider when defining terrestriality in fishes
All fishes, if put on land, have the capacity to move their bodies against the forces of gravity and friction. How each species coordinates body and fins and how effectively they move over land varies remarkably and makes the classification of 'terrestriality' among fishes challenging. A recent paper by Turko et al. (2021) scores fishes' terrestrial performance using a scoring metric that combines physiological capacities (emersion tolerance) with a land-

use score based on drivers that either push an animal or pull an animal out of water (push: drought, intolerable water chemistry; pull: food, reproduction and habitat). The combination of these factors are used to categorize fish as more or less 'amphibious'. The present Review aims to expand on the land-use score aspect of this classification scheme by further exploring the biomechanical performance of fishes in terrestrial environments. For animals that voluntarily emerge or remain on land as water leaves them, we propose two idealized metrics that can be considered to describe and compare fish terrestrial motion. The first is effective performance: is there a significant directional motion to the behaviour? More clearly put, is the animal moving on land in place or locomoting over land? The distance ratio, which measures the linear distance of the center of mass (CoM) as a proportion of the total distance travelled by the CoM, can be used to quantify the effectiveness of a behaviour. Straight-bodied, crutching fishes such as mudskipper or the jumping blennies score very high with this metric, and armoured catfish that oscillate side to side more than they move forward score low (Bressman et al., 2018; Kawano and Blob, 2013; Pace and Gibb, 2011). Measuring distance travelled per locomotor cycle also helps quantify performance between locomotor modes (see Glossary). For example, jumping fishes can travel many body lengths per jump whereas walking fishes tend to require many steps to cover the same relative distance. The second idealized metric is effective distance: in a given emersion event, how far do fish travel over land? Amphibious fishes are diverse in their activity level once on land; for example, mangrove rivulus (*Kryptolebias marmoratus*) spend their time out of water relatively inactive, buried in leaf litter and logs, whereas swamp eels (Synbranchidae) perform terrestrial excursions to hunt for prey (Sayer and Davenport, 1991; Taylor, 2012). As a metric, effective distance captures the activity level of the animal once on land. A combination of scores across these metrics would then be a possible comparative tool to assess the terrestrial locomotor ability of a given fish species. Although there are many excellent papers that make specific biomechanical analyses of individual species, much of the literature is highly descriptive, so it is difficult to assess the idealized metrics listed above in a meta-analysis. We encourage future studies of amphibious fishes to consider quantifying each species for effective performance and effective distance. Applying a framework that allows comparison between species would be useful when determining the relevance of a newly described behaviour in the context of fish terrestrial performance. We do recognize that this is a non-trivial task, as the natural behaviour of many fish species is not well documented.

Phylogenetic patterns of fish terrestrial locomotion
To understand how patterns of diversity in fish terrestrial locomotion might provide insight into what constrains performance, we examined fish terrestrial locomotion across the actinopterygian tree. We used a recently generated tree of fishes (Rabosky et al., 2018), open source data (Sayer and Davenport, 1991; Wright and Turko, 2016) and several R packages (Paradis and Schliep, 2019; Revell, 2012; Wickham et al., 2016) to compile and visualize these data. We categorized fish using five 'alternate' metrics as proxies for the effective performance and effective distance metrics (body shape, behaviour, active anatomy, activity level and skin anatomy; Table 2). Behaviour, active anatomy, body shape and skin anatomy all contribute to how fish locomote and impact effective distance. Behaviour, active anatomy and activity level determine how far a fish can travel overland thus representing effective performance. Each of the five 'alternate' metrics were calculated using categorizations or calculations from peer-reviewed data, data from FishBase, the

Table 1. Summary of amphibious behaviours in fishes and select citations

Behaviour	Citations
Axial-based locomotion	
Sinusoidal body undulations and oscillations	Kinematics: Ellerby et al. (2001), Gibb et al. (2011), Gillis (1998), Horner and Jayne (2014); vertebral morphology: Ashley-Ross et al. (2014), Mehta et al. (2020); muscle activation: Bressman et al. (2019), Ellerby et al. (2001), Gillis (2000), Horner and Jayne (2014)
Jumping	Kinematics: Bressman et al. (2016, 2019), Graham (1970), Graham et al. (1985), Hsieh (2010); Perlman and Ashley-Ross (2016), Swanson (2004), Taylor (2012); mating displays: (Clayton and Vaughan, (1988), Stebbins and Kalk (1961); with fins as positioners: Graham (1970), Nieder (2001)
Appendage-based locomotion	
Crutching	Kinematics: Gordon et al. (1968), Harris (1960), Kawano and Blob (2013), Pace and Gibb (2009), Sayer (2005), Wang et al. (2013); using tail for escape and jumping: McInroe et al. (2016), Swanson (2004), Wang et al. (2013)
Appendage-axial locomotion	
Fins as support and stabilizers	Bressman et al. (2019), Foster et al. (2018), Standen et al. (2016, 2014); with opercular spines: Davenport and Abdulmatin (1990)
Modified fins for suction	Blob et al. (2006, 2007), Cediel et al. (2008), Flammang et al. (2016)
Underwater walking	
Extinct fishes	Boisvert (2005), Clack (2009), Coates et al. (2008), Edwards (1989), Gunter (1956), Lebedev (1997), Shubin et al. (2006)
Extant fishes	Aiello et al. (2014), Edwards (1989), Fox et al. (2018), Holst and Bone (1993), Jamon et al. (2007), King et al. (2011), Petersen and Ramsay (2020), Pridmore (1994); up waterfalls: Blob et al. (2006, 2007), Crawford et al. (2020), Flammang et al. (2016), Schoenfuss and Blob (2003)

See Table S1 for a complete list of literature describing locomotion organized by species.

Encyclopedia of Life and the Global Biodiversity Information Facility, and occasional use of fish ID and aquarium guides and nature documentaries (Table 2; see Fig. S1 and Supplementary Materials and Methods for details on calculation of locomotor metrics and Table S1 for phylogeny organization details).

To move on land, most genera of amphibious fish jump, laterally undulate or tail push (Fig. 3A,B; Fig. 3A, jump, dark grey highlights; lateral undulation and tail push, white highlights with the exception of two species that remain). More specialized behaviors such as walking or 'crutching' appear only a few times in the tree (Fig. 3A, medium and light grey highlights, respectively). Amphibious fishes make up a small subset of the complete fish phylogenetic tree and this must be taken into consideration when discussing how phylogenetic position impacts the distribution of terrestrial modes of locomotion across fishes. In the amphibious subset of fishes, two interesting patterns emerge. First, although relatively rare, a tetrapod-like walking mode, where the fish uses its fins in a contralateral stepping pattern, appears in the most basal extant ray-finned fish, *P. senegalus* (Fig. 3A, medium grey highlight), and recurs throughout the tree, likely evolving independently in each clade. The early diverging positions of fish that walk, and the number of times they

appear to have evolved, suggests there is an affinity for tetrapod-like fin–body coordination when moving overland. The coordinated underwater walking ability in chondrichthyans also supports the idea that an ancestral control pattern may drive these behaviours (Lucifora and Vassallo, 2002; Pridmore, 1994; see 'Neural control in a terrestrial environment', below). In contrast to walking, a second pattern emerges in the relatively tight distribution of jumping fishes. Jumping is the most common mode of locomotion on the genera tree and appears predominantly in the most derived fishes (Fig. 3A, dark grey). Most jumpers appear to be confined to two closely related groups of fishes, the Gobiesociformes and Blenniformes (sister taxa) and the Atherinomopha (Altherinoformes and Cyprinodontiformes, sister-taxa); this close grouping of jumping capability suggests that phylogenetic inertia (see Glossary) is a factor for the distribution of this trait. A closer look at the tree, however, shows members of the Charactiformes (Hoperythrinus and Eythrinus), a group distantly related to the derived jumpers, also use jumping as a locomotor strategy. In addition, the closely related Gobiesociformes clingfishes (Gobiesox and Tomicodon) do not jump. These two anomalous groupings within the amphibious fishes suggest that phylogenetic inertia may not be the only thing affecting the distribution of jumping
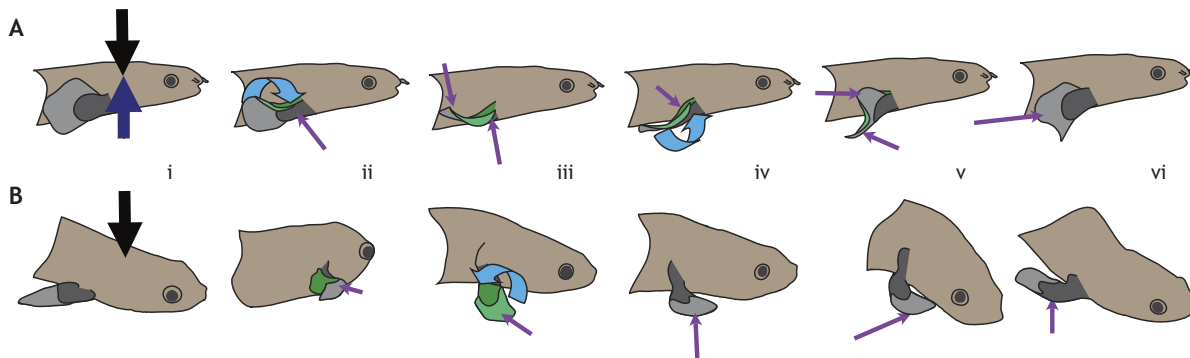

Fig. 1. Changed force environments: water versus land. (A) In water, the buoyancy of a fish (dark blue arrow) counteracts the effect of gravity (black arrow) such that the resulting forces felt by the fin (purple arrows) are only those of the fin pushing against the water. As the fin moves through the power stroke (Aiv–vi) and recovery stroke (Ai–iii), the force of water on its surface changes direction but remains relatively orthogonal to the fin surface. (B) On land, the full force of gravity is felt by the fin as it is loaded during a single step. In addition, the fin is bent at the fin ray (light grey/green)–radial (dark grey/green) joint (Biii–vi), causing the forces experienced by the fin to act in a potential bending moment on the fin bones on either side of the joint. Fin swing phase occurs at Bi–ii. Green represents the medial side of the fin and grey represents the lateral side of the fin. The wider light blue arrows depict the direction of fin motion.
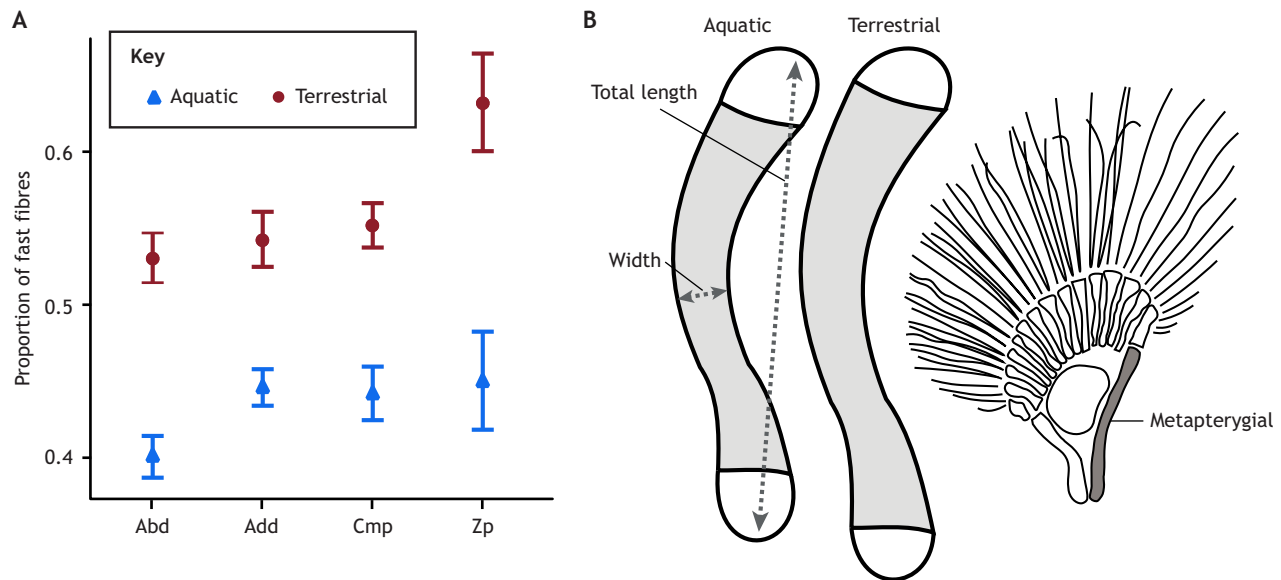
Fig. 2. Muscle fibre type and bone morphology changes in *Polypterus senegalus* after 5 weeks on land. *(A)* Muscle tissue in the fins of *P. senegalus* has more fast fibres (anaerobic, glycolytic fibers) following terrestrial acclimation (from Du and Standen, 2017) and (B) the metapterygial fin bone is also longer, wider and more ossified following terrestrial acclimation (modified from Du and Standen, 2020). Points in A are means±s.e.m. Grey shading in B represents the ossified portion of the bone. In A, pectoral fin muscle abbreviations are as follows: Abd, abductor; Add, adductor; Cmp, coracometapterygialis; Zp, zonopropterygialis.

locomotion in fishes. The fairly well-distributed occurrence of tail pushing and lateral undulation also supports the idea that broader constraints such as body size, shape and plasticity can act across phylogenetic groups to determine locomotor mode independent of phylogenetic inertia (Fig. 3A,B). Looking directly at characteristics that impact a fish's ability to locomote terrestrially helps broaden our understanding of what drives effective terrestrial locomotion.

What drives effective terrestrial locomotion?
As with swimming biomechanics, the laws of physics, combined with the size, shape and anatomical specialization of a fish, will determine locomotory performance in a terrestrial environment. Maintaining body posture, supporting body weight and moving mass all require the muscles and skeleton to produce locomotor forces (ground reaction forces, GRF). The capacity of the muscles to produce forces and torques to accomplish these tasks has evolved to facilitate the preferred mode of motion used by the individual.

Size
The more massive an animal is, the greater the forces it must produce to successfully move overland. Because body mass increases with length^3 (L^3) and muscle force increases with its cross-sectional area (L^2), the capacity of a large fish to lift its weight efficiently is reduced compared with that of a smaller fish. Large terrestrial animals such as elephants reflect this, having evolved posture that relies on the skeleton, rather than muscle, to support load, thus reducing locomotor costs (Biewener, 1989a,b). Even within the fishes that do have the capacity to move overland, patterns of size related to mode of locomotion appear to exist. For example, most fishes that use jumping modes are in the smaller size range (Fig. 4). Although, as mentioned earlier, it may be difficult to rule out phylogenetic inertia on these patterns, the amount of force required to lift an entire body off the ground becomes prohibitive at larger body sizes. One might conclude that larger fishes choose non-ballistic modes of terrestrial locomotion because these modes require less muscle mass, maintenance and effort than ballistic jumping. The reduced muscle mass would limit the amount of

energy an individual would have to use per distance travelled. Evidence of this trade-off (see Glossary) can be seen in an ontological context in gobies, who lose their capacity to use burst performance to climb as they grow (Blob et al., 2007). Adult gobies develop specialized sucking disks to climb, because body muscles alone do not permit burst climbing at larger sizes (Blob et al., 2007). A similar pattern exists in snakehead (*Channa argus*), where jumping is prevalent when they are young but disappears when they are adults (Bressman et al., 2019). It seems as though the physiological limits of muscle force production and musculoskeletal anatomy create size-specific strategies for terrestrial locomotion in amphibious fishes.

Shape
The body shape of amphibious fishes is highly variable and likely dictates preferred terrestrial locomotor mode. In general, fishes at the extreme ends of the elongation spectrum (tadpole shaped and eel-like) are less active than the other body shapes and activity tends to decrease as elongation increases (Fig. 3D, clockwise from fusiform to elongate). Locomotor mode also changes with body shape: tadpole-shaped fishes move mainly using the tail pushing method, whereas lateral undulation is the primary mode of locomotion for extremely high aspect ratio, eel-like fishes (Fig. 3B). Jumping is underrepresented in both tadpole-shaped and longer fish species, but is the dominant behaviour in fusiform-shaped fish. Finally, forms of locomotion involving tetrapod-like fin–body coordination such as crutching and walking are only seen in long or elongate fishes (Fig. 3B). The complex relationships between phylogenetic relationship, body shape, locomotor mode and activity level are difficult to parse. Except for the jumpers, which are mostly fusiform, the broad distribution of body shape and locomotor mode suggests that phylogenetic inertia exists asymmetrically on the amphibious fish tree, canalizing locomotor mode in some groups (the jumpers) but not in others.

Even within jumping, it is interesting to think about what contributes to differences in performance. Just as size or mass seems to dictate a cut-off for which fish species are actively

Table 2. Categories for phylogenetic tree visualization

Category	Description
Body shape	
Tadpole	Wide large anterior with a tapering tail; AR>5+HH>0.925×MH
Fusiform	Streamlined and torpedo shaped; AR<4 or AR<5.5+HH<0.85×MH
Long	Similar length to a fusiform fish (see Glossary), less hydrodynamic; 4.0<AR< 6.8
Elongate	Longer abdomens, tails or both; 6.8<AR<8.5
Eel-like	Extreme elongation, often with reduced or no pectoral fins; AR>8.5
Skin anatomy	
Armour	Thick bony scales or plates along the body
Scales	Thin scales covering most of the body
Skin	Few or no scales
Active anatomy	
Axial	Using a combination of head, body and tail
Appendicular	Using their fins
Both	Using both axial and appendicular anatomy
Activity level	
Active	Voluntarily move between water and land freely and often
Both	Often stranded on land owing to seasonal or tidal changes, often active during that time
Remains	Often stranded owing to seasonal or tidal changes; hunker down and wait
Behaviour	
Crutching	Contralateral fins used simultaneously to lift the body off the ground and push it forward over the fins; both sets of paired fins are used for support through the stepping cycle; tail can also be used, planting to alternate sides of the body and pushing the fish forward over the fins
Walking	Alternating planting of contralateral fins (2 or 4), which help lift and push the body forward; this motion can be aided by the tail helping to push the body over a planted fin.
Tail pushing	Body bends at a single point, pulling the tail forward to plant alongside the anterior portion of the body; the tail then pushes the animal forward without an aerial phase or constant support from a fin
Lateral undulation	Entire body is used and bends with exaggerated side-to-side movements
Jumping	Body is launched off the ground

AR, aspect ratio of standard length to maximum body height (MH); HH, head height from the highest point on the neurocranium to the ventral surface of the fish.

terrestrial or jump effectively (Fig. 4), our data show that body length impacts locomotor mode, favouring fusiform jumpers. Within fusiform jumpers, previous studies have shown some ambiguity between length and performance metrics associated with terrestriality. Fineness ratio, which is the length of an animal divided by its width, appears to increase with terrestrial lifestyle in the comb-toothed blennies (Salariini) (Gibb et al., 2013); however, in a subsequent study including 11 species of killifishes (Cyprinodontiformes), fineness ratio as well as other morphological measures did not predict emersion behaviour (Minicozzi et al., 2020). We can turn to physics to help explain how differences in body length might explain the contrast in results between studies. As fineness ratio increases, controlling body motion throughout the preparatory and launch phase of a jump becomes challenging. When a fish jumps, it must control its body position in the air as it leaves the ground. In the preparatory phase of the jump, the body begins to be lifted off the ground. The greater the length of the body that is in the air, the farther the centre of mass of the elevated portion of the body (CoM_{AIR}) gets from the point of ground contact. As the distance between the CoM_{AIR} and the ground (or centre of pressure) grows, the moment arm of the CoM_{AIR} increases, increasing the torque it produces and the muscle force required to control the body mass that is off the ground. This increased torque would make it difficult for very elongate animals to stabilize their bodies during the jump.

Stability and maneuverability are a constant trade-off in an aquatic environment, where fish balance their centre of mass (CoM) with their centre of buoyancy (CoB; see Glossary) to optimize body position (Chadwell et al., 2012a,b; Drucker and Lauder, 2005; Eidietis et al., 2002; Lauder and Drucker, 2004; Standen, 2010; Standen and Lauder, 2005, 2007; Webb, 2006; Webb and Weihs, 1994). Because the physical forces experienced in terrestrial and aquatic environments are so different, traits that confer stability in an aquatic environment may not do so in the terrestrial realm. For example, fish that are medio-laterally flattened, such as the bluegill sunfish (*Lepomis macrochirus*), resist roll torques in water, but immediately roll onto their side on land (Schrank and Webb, 1998). In contrast, fish with wide bellies and ventrally located pectoral fins may be less streamlined during swimming, but are very stable in an upright position on land (i.e. sculpins, Cottoidea and the walking catfish, *Clarias batrachus*; Bressman et al., 2018, 2019; Johnels, 1957). A body shape that maintains its posture between aquatic and terrestrial habitats may make it easier for fish to coopt existing swimming motor patterns for effective terrestrial locomotion (see 'Neural control in a terrestrial environment'). In hypoxia-induced emersion studies, differences in body morphology were determined to affect the ability of fish to emerse from water. Both the rigid build of the sea scorpion *Taurulus bublis* and the slender build of the intertidal rockling *Ciliata mustela* reduce emersion performance (the ability to leave the water) of these species relative to that of the robust and flexible blenny *Lipophrys pholis* (Davenport and Woolmington, 1981). In this way, the physical characteristics of particular body shapes may provide excellent exaptive opportunities (see Glossary) for fishes to become terrestrial.

Specialization

Morphological specializations often help fishes to locomote terrestrially. For example, mudskippers have specialized pectoral and pelvic fins that they use to execute a highly effective and unique crutching motion (Gordon et al., 1968; Kawano and Blob, 2013; Pace and Gibb, 2009; Wang et al., 2013). The climbing perch, unlike the majority of fish with fusiform shapes, does not jump, but rather 'walks' using a uniquely formed operculum that is jointed and spined, such that the fish can gain purchase as it uses its body to push itself over each spine (Davenport and Abdulmatin, 1990). Even the heavily armoured catfish have been hypothesized to have specialized bony plates that allow them to outperform similarly shaped animals without bony plates (Bressman, 2020). Sometimes, specialized morphological adaptations come at a cost to other forms of locomotion. *Periopthalmus koelreuteri* have modified short and stiff pelvic fins that improve body support for walking but limit its ability to climb because it no longer has the suction-producing pelvic plate that is used by closely related species (Okamoto et al., 2018; Wicaksono et al., 2016). Despite potential trade-offs, specialized morphologies may allow fish to take advantage of selective niches; for example, the pectoral and pelvic fins of the rockskipper, *Alticus kirkii*, end in hooks to aid in climbing steep rocks (Zander, 1972).

Specialization in muscle fibre type also exists in closely related species with different life-history patterns. For example, in Hawaiian climbing gobies, species using power-burst locomotion have a greater proportion of white (anaerobic, fast-twitch) muscle (see Glossary) compared with those using an 'inching' locomotion, which have more red (aerobic, slow-twitch) muscle (see Glossary; Cediel et al., 2008). Amphibious fishes that use very different locomotor
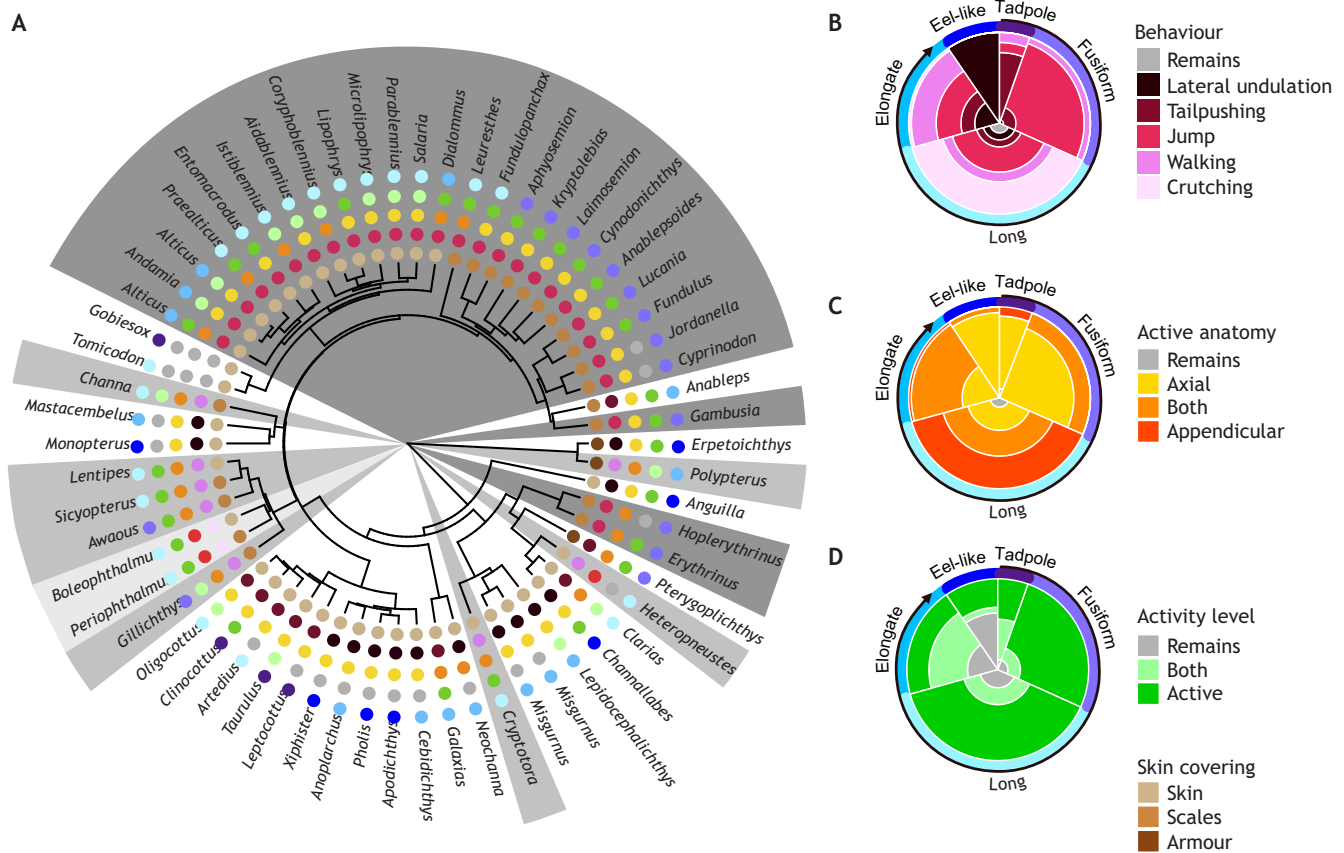
Fig. 3. Phylogenetic tree of amphibious fishes. (A) Five sets of categorical variables are mapped with the genera of interest (Table 2). The earliest deriving groups start at 03:00 h on the phylogeny with *Erpetoichthys* and move clockwise around the tree to the latest deriving genus, *Gambusia*. Earlier diverging amphibious fish mostly tail push and laterally undulate, with more specialized modes such as walking and crutching appearing throughout the earlier half of the tree. Later-derived fishes mostly move terrestrially by jumping. Highlights in A represent remains/lateral undulation/tail pushing (white) jumping (dark grey), walking (medium grey), or crutching (light grey). Note that the coloured circles in A represent the categories detailed in B–D. (B–D) Polar stacked histograms showing the relationship between body shape and activity level, active anatomy and behaviour. Width of each slice in the plot is proportional to the number of species in each body shape category (i.e. a narrower slice means fewer amphibious fish in that category). Height of each coloured bar (or distance from the center of the polar plot to the outer edge) represents the percentage of species within each body shape category that fall into each sub-category (i.e. behaviour in B, active anatomy in C, activity level in D). In general, body aspect ratio (ratio of standard length to maximum body height) increases from tadpole at 12:00 h, continuing clockwise around the plot (black arrow) to eel-like. Tadpole, fusiform and long fishes overlap somewhat in aspect ratio, but have additional differences in body shape defined by the relationship between head height and maximum body height (see Table 2 and Supplementary Materials and Methods for details).

modes across environments may require different muscle fibre arrangements to maximize performance in each environment, leading to a potential trade-off of performance in one environment or the other, or both (Greer-Walker and Pull, 1975; Grgic and Schoenfeld, 2018; Wright and Turko, 2016). Different force conditions can lead to a plastic response of muscle fibres (discussed below), which may help individuals to meet the demands of new environments; however, plasticity will depend on how long an animal spends in one environment or how often they switch between environments. In addition, plasticity may come with high energetic costs associated with generating or breaking down tissues (Wright and Turko, 2016).

Tissue plasticity

The vastly different environmental conditions of water and land mean that fish that spend more than a few seconds on land require physiological mechanisms capable of managing processes that effect tissue function such as gas exchange, ion balance, hydration and temperature (Chew and Ip, 2014; Damsgaard et al., 2020; Sayer, 2005; Wright and Turko, 2016). Amphibious fishes show a remarkable ability to restructure their physiological support systems to maintain homeostasis in a terrestrial environment, resulting in an

increase in the amount of time they can spend on land (Wright and Turko, 2016). The increased exposure to terrestrial forces, in turn, elicits a plastic response in the musculoskeletal system, which can drive biomechanical performance (McFarlane et al., 2019; Standen et al., 2014).

How plasticity alters performance is a complex and nuanced process. The evolutionary history of an animal dictates its size, shape and specialization, which, added to the novel physical and physiological constraints of the terrestrial environment, provide the canvas for adaptive selection. The extent of the plasticity of each trait, whether for maintaining physiological homeostasis or remodelling musculoskeletal systems, will impact the performance capacity of the individual. Environmental triggers of physiological plasticity may have off-target effects that benefit or hinder biomechanical performance. For example, exposure to hypoxic conditions, which might occur in fishes that cannot perform adequate gas exchange on land, can trigger a plastic response that depresses metabolism, limiting resources available for muscle performance (Bickler and Buck, 2007) or preserving them for future locomotor performance (Rossi and Wright, 2020). In addition, it appears that exposure to fluctuating environmental conditions in
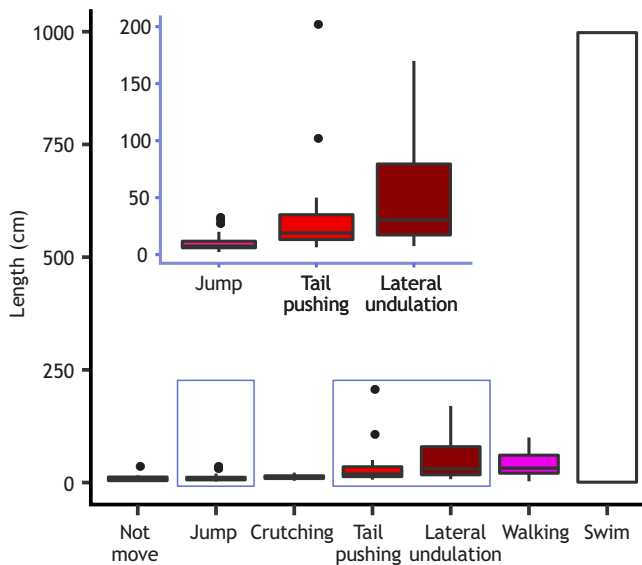
Fig. 4. Lengths of amphibious fishes compared with swimming fishes. Amphibious fishes (filled bars) are small compared with the length distribution of all fishes (white bar). Jumping fishes are small compared with all other amphibious fishes. Inset shows the same data focused on jumping, tail pushing and laterally undulating fishes. Boxplots show means and 25th and 75th percentiles.

juvenile mangrove rivulus limits their phenotypic flexibility as adults (Rossi et al., 2020). These data suggest that an organism's ability to respond to a novel environment is a delicate combination of evolutionary history, developmental history and competing plastic responses at the individual level.

Bone dynamically remodels when exposed to loading, generally increasing in volume with increased loading and resorbing (see Glossary), with decreased loading (Burr et al., 2002; Chamay and Tschantz, 1972; Hall and Herring, 1990; Lang et al., 2004; Lanyon and Rubin, 1985; Nowlan et al., 2010). Dynamic loading (see Glossary), which occurs during movement, tends to have a larger impact on bone remodelling compared with static loading (see Glossary), which occurs when the animal is still and can even lead to bone resorption in some cases (Lanyon, 1992; Lanyon and Rubin, 1984, 1985; Robling et al., 2001). In addition to the type of loading, bone plasticity is also affected by the duration and number of loading events (Gross et al., 1997; Hsieh and Turner, 2001; Judex et al., 1997; Warden and Turner, 2004), suggesting that the amount of time a fish spends on land will impact its plastic response. Although much of what we know about bone remodelling is taken from mammalian models, fish bone also has the capacity to remodel (Atkins et al., 2014; Cardeira et al., 2018). Aquatic exercise in fishes results in greater osteoblastic activity (increase in bone development), earlier ossification and higher mineral content than observed in non-exercised fish (Deschamps et al., 2009; Totland et al., 2011). Terrestrial loading in the fish *P. senegalus* causes changes in the shape of the bones supporting the pectoral fin after 8 months on land, and differences in fin bone structure after only 5 weeks (Du and Standen, 2020; Standen et al., 2014). How these shape changes impact functional performance is difficult to quantify, but it is known that the gill arches of mangrove rivulus show an increase in collagen associated with endochondral bone growth after terrestrial loading, and this is accompanied by a measured increase in functional stiffness of the arch, suggesting these plastic responses have positive performance outcomes (Turko et al., 2017).

Fish muscle also responds plastically to force environment or exercise. Endurance training in swimming fishes increases both the size and number of aerobic muscle cells, as well as the size of glycolytic cells despite the slow speed of the training (Davison, 1989, 1997). Muscle capillarization also increases with aquatic exercise, suggesting muscle plasticity is accompanied by changes to the necessary support structures that supply oxygen and fuel and remove waste products (Sänger, 1992; Sänger and Stoiber, 2001). In terrestrial environments, burst-like exercise in walking *P. senegalus* results in increases in the number of fast-twitch fibers in the pectoral fin musculature (Fig. 2; Du and Standen, 2017). Mangrove rivulus also show marked changes in both aerobic and glycolytic body muscle anatomy and improvement in terrestrial performance after acclimation to terrestrial environments (Brunt et al., 2016; McFarlane et al., 2019). Thus, fish tissues appear to be highly responsive to changes in environmental forces, suggesting that plasticity contributes to increased performance capacity in terrestrial environments.

A simplified view of musculoskeletal plasticity would predict that muscle and bone changes that occur due to exposure to the novel terrestrial environment will increase locomotor performance. This is because both muscle and bone respond to accommodate mechanical loading forces. Changes in muscle force production capacity and bone strength or shape (mechanical advantage) would provide an individual with more effective access to terrestrial environments, thus exposing them to the associated adaptive selective pressures.

Relating drivers of effective terrestrial locomotion to the idealized metrics

It is difficult to relate large-scale phylogenetic patterns of fish terrestrial capacity with the smaller comparative metrics of performance based on the physical constraints of body shape and size. Even more difficult to interpret in a larger-scale phylogenetic context are performance metrics that change as the result of the shorter-term plastic response of animals exposed to novel environments. The idealized metrics of effective performance and effective distance help to focus data collection such that it can be used in a reliable comparative context to support and fine tune scoring structures such as those proposed by Turko et al. (2021). Organization of data in this way can then be applied to broader-scale studies interested in evolutionary constraints or universal biomechanical control principles.

Neural control in a terrestrial environment

Terrestrial and aquatic locomotion require different locomotor modes; even when the same propulsive structures are used, they are seldom used identically. For example, *P. senegalus* uses different pectoral fin and body movements for aquatic locomotion than for terrestrial locomotion (Standen et al., 2016, 2014). Although many studies describe aquatic and terrestrial locomotor modes (Table 1), few report how neuromuscular control changes between environments. In all environments, neural patterns (a set of neuronal output signals from one or more neurons with a specific firing sequence) are generated by neural circuits, a particular set of interconnected neurons that may include brain centres, central pattern generators (CPGs), sensory neurons and motor neurons (Box 1). Neural patterns for cyclical locomotion are the result of interactions between CPGs, local sensory feedback (e.g. proprioceptive feedback made directly to CPGs) and top-down sensory feedback [i.e. sensory inputs that are integrated in the brain (pallium) before being passed to spinal CPGs] (Fig. 5) (Goulding,

Box 1. Physiological components of a neural control system

The neural components that control rhythmic locomotion (e.g. walking, running, swimming, hopping) are shared across the animal kingdom. The brain, spinal cord and sensory systems work together to produce and modify motor signals required for locomotion. Locomotion is initiated by signals from motor command areas in the mesencephalon (mesencephalic locomotor region, MLR) and diencephalon (diencephalic locomotor region, DLR) of the brain (Dubuc et al., 2008; El Manira et al., 1997). Low-level electrical stimulation of the MLR elicits swimming in lamprey (Sirota et al., 2000) and walking in salamanders (Cabelguen et al., 2003); likewise, DLR stimulation initiates locomotion in mammals and lamprey (El Manira et al., 1997). When MLR stimulation is increased, lamprey swim faster and salamanders stop walking and commence swimming. Thus, these motor command areas adjust the speed and mode of locomotion and may be used independently in different behaviours. The reticulospinal neurons carry signals from the MLR and DLR to central pattern generators (CPGs). CPGs are neural circuits (sets of interconnected neurons) that, in isolation, generate appropriately timed neural patterns for rhythmic locomotion (Grillner and El Manira, 2020). The organization of a CPG neural circuit defines the rhythm and left–right coordination of a stereotyped locomotor pattern. In CPGs, the neural pattern sequentially activates motor nerves and, thus, muscles. Because CPGs generate stereotyped behaviour, any rhythmical behavioural modifications require neuroplasticity of the CPG output. CPG organization is plastic within hours (tritonia; Sakurai and Katz, 2009) or days (cat; Barrière et al., 2010, 2008; Gossard et al., 2015; Martinez et al., 2011), whereas synaptic transmission is plastic almost instantaneously (Grillner and El Manira, 2020). Short- and longer-term neuroplasticity allow animals to generate effective locomotion in the face of environmental change or injury. Both the motor neurons themselves and sensory feedback (information about the environment gathered using specialized sensors that is passed directly to the CPG or motor neuron or is passed to integrative brain centers such as the cortex/pallium) influence the background excitability, neural pattern and left–right coordination of CPGs to suit the current environment. Fish additionally have 'escape circuits', wherein reticulospinal neurons (specifically specialized Mauthner cells) are activated by a variety of sensory inputs and pass a neural pattern (sometimes as simple as a single action potential) directly to motor neurons to initiate escape behaviours (Domenici and Hale, 2019). Like the neural circuits used for rhythmic locomotion, the resulting escape behaviour depends on the type of sensory stimuli received and is subject to plasticity of neural synapses (Medan and Preuss, 2014).

2009; Rossignol et al., 2006). The neural pattern is passed from CPGs to motor nerves, which elicit muscle contractions to generate locomotor movements that are constrained by the physical environment. Locomotion may also be created, as in aquatic escape responses, by a neural pattern (potentially a single action potential) that is passed from Mauthner neurons (specialized neurons in the brain stem) directly to motor nerves. Regardless, amphibious fish must accomplish effective terrestrial locomotion using bones, muscles, neural control and sensory systems that originally evolved in an aquatic environment. For each of these systems, plasticity may be a key facilitator in making the water-to-land transition a success.

Just as for bones and muscles (e.g. Du and Standen, 2017, 2020; see above), the neural control system of fishes is plastic in response to changing force environments (Mes et al., 2020; Teles et al., 2016). For example, increased swimming exercise in fishes leads to telencephalic neurogenesis and changes in synaptic performance (Mes et al., 2020), and terrestrial exercise generates neurogenesis and learning in amphibious fish (Rossi and Wright, 2021). Presumably, then, neural control could also remodel in fishes

exposed to environments that demand novel performance. Here, we suggest four ways in which neural control could meet the demands of a terrestrial environment (Fig. 5): (1) aquatic neural circuits and neural patterns could be used unchanged, with the environment shaping or confining the resulting locomotor movements; (2) aquatic neural circuits and driving neural patterns remain unchanged, but pattern parameters such as frequency and amplitude are modulated; (3) aquatic neural circuits could generate a completely novel neural pattern; or (4) new neural circuits could form and generate a novel neural control pattern. These four possibilities are discussed in more detail below.

Aquatic neural control circuits are used unchanged

A single neural circuit and unchanged neural pattern may be sufficient to control successful locomotion in both aquatic and terrestrial environments (Fig. 5A–C). In this case, with no changes in muscle activity (Fig. 5B), terrestrial forces would alter the timing of kinematic output relative to muscle activity and produce an effective, but altered, locomotor mode. Although to our knowledge this has not been studied in amphibious fish, there is some evidence for this idea in lizards, which use similar muscle activity while walking along an incline and on flat ground, with unique kinematics in each environment (Foster and Higham, 2014). Human postural muscles also activate similarly to stabilize sitting in response to a variety of perturbations (Forssberg and Hirschfeld, 1994).

Neural control circuits and basic patterns remain unchanged, but pattern parameters are modulated

The same neural circuit may change intensity and shift timing while keeping the same underlying neural pattern (e.g. a travelling wave passed anterior to posterior; Fig. 5C) to allow an amphibious fish to locomote on land. For example, increased electrical stimulation to the lamprey brain (mesencephalic locomotor region; see Box 1) causes a higher frequency and intensity of muscle activity resulting in greater body bending, presumably through the same set of neural connections (Sirota et al., 2000). The shift from an aquatic to a terrestrial environment elicits similar increases in muscle activity frequency and intensity, resulting in increased kinematics in eels (Gillis, 1998, 2000). Thus, the hypothesis that terrestrial and aquatic locomotion are supported by the same neural pattern with altered timing and intensity is supported by eel data and may be a common feature of terrestrial locomotion in elongate amphibious fish.

Novel neural control patterns

Aquatic and terrestrial locomotion in amphibious fishes could use the same neural circuit, but a novel neural control pattern (Fig. 5D). For example, a spinal cord model implemented in an amphibious salamander robot shows that a single neural circuit can explain the differences in neural pattern between swimming and walking with a simple change in CPG input intensity (Ijspeert et al., 2007). As CPG input intensity increases, a threshold is reached and the body wave pattern changes from a travelling wave to a standing wave. In biological systems, electromyography can be used to measure motor outputs but its ability to confirm neural control strategies is challenged by the role of sensory feedback. The feedback from sensory systems of living animals can alter CPG and brain signals, changing neural control patterns. In addition, sensory systems that fine-tune neuromuscular control may have an altered function in terrestrial environments, limiting our ability to determine whether changes in locomotor mode are due to novel neural circuits (Fig. 5E) or modulation of existing neural circuits by altered sensory feedback. However, there are a few compelling examples of
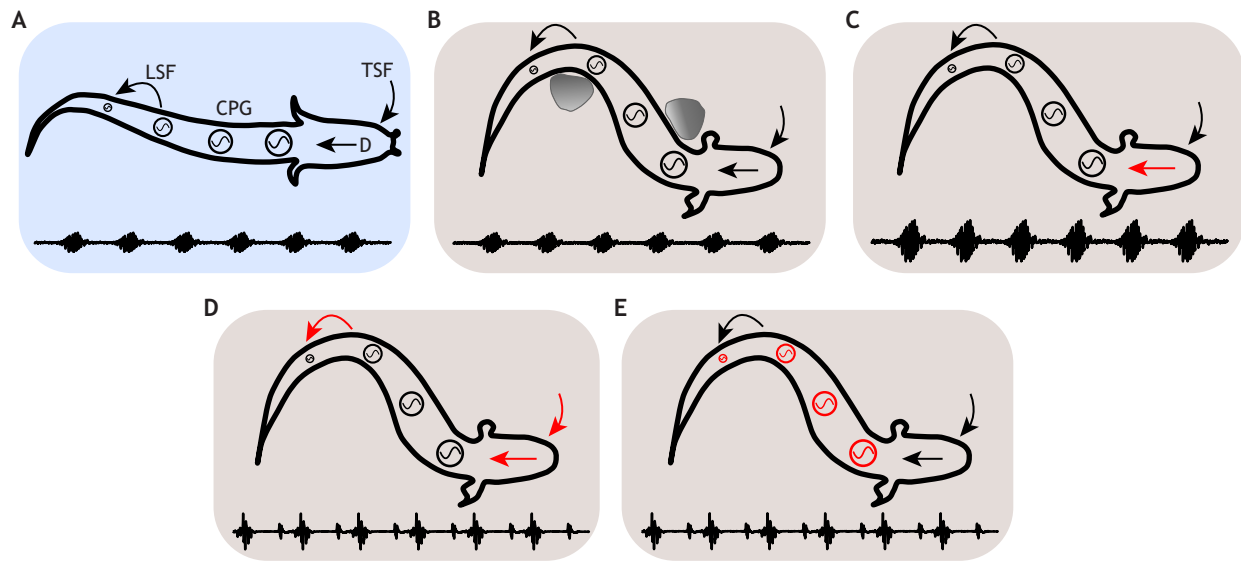
Fig. 5. Changes in neural control for terrestrial behaviour. (A) Neural control elements and the aquatic muscle pattern. Successful terrestrial locomotion could result from an existing aquatic neural control pattern (B,C), or a novel control pattern (D,E). In each panel, unchanged neural elements are in black. Although still present and functioning, these elements would not be the main driver of a new mode of locomotion. Changed element(s) in each panel are red. (B) An unchanged aquatic neural control pattern may be constrained by the environment (indicated by grey rocks adjacent to the fish). (C) The aquatic neural control pattern may be amplified by increased drive (indicated by increased muscle activity intensity). (D) Sensory feedback and/or increased drive could modulate the aquatic neural control circuit to elicit a new neural control pattern. (E) A novel neural control circuit could generate a novel neural control pattern. CPG, central pattern generator; D, drive to CGPs; LSF, local sensory feedback; TSF, top-down sensory feedback. In each panel, an example of resultant muscle activity from a single muscle is shown at the bottom. Background colour represents the environment (blue, aquatic; brown, terrestrial).

modified neural patterns. Terrestrial jumping in amphibious killifish likely uses a different or highly modified neural pattern, because it is powered by additional bursts of muscle activity that are not present during aquatic escape responses (Perlman and Ashley-Ross, 2016). Another compelling case for a novel neural pattern driving terrestrial jumping comes from the mudskipper (Swanson, 2004). This species produces two kinematically distinct escape responses. One is most common in the aquatic environment and the other in the terrestrial environment. However, these behaviours are occasionally observed in the contrasting environment, suggesting that two distinct neural patterns exist. Studies where anatomically similar species of amphibious fish exhibit different terrestrial modes may provide another opportunity to isolate examples where novel neural patterns in fishes have evolved (see blennies and sculpins; Bressman et al., 2018; Hsieh, 2010). However, it may be necessary to measure neural or motor patterns in a variety of force environments with and without sensory input to better understand how locomotor control is mediated across aquatic and terrestrial conditions. Further, we are unable to determine whether the changes in neural control pattern are the result of an existing neural control circuit or a novel neural circuit (Fig. 5D,E) for any of the above examples. Modelling these systems using a CPG-based approach (Ijspeert et al., 2007) or directly recording from CPGs and associated interneurons (as has been done for the lamprey; reviewed in Grillner and El Manira, 2020) may elucidate these differences.

Although this review focuses on terrestrial locomotion, underwater substrate-based locomotion has evolved several times in a variety of fishes (Table 1). Most of these studies focus on the kinematics of these behaviours with few recordings of muscle activity (but see Aiello et al., 2014). Many of these modes are unique adaptations that permit substrate-based locomotion for benthic species (e.g. skates and flatfish; Fox et al., 2018; Holst and Bone, 1993), whereas others bear some resemblance to hexapodal (e.g. sea robin; Petersen and Ramsay, 2020) or tetrapodal (e.g.

frogfish and lungfish; Edwards, 1989; King et al., 2011) modes. Like the study of terrestrial locomotion in fish, these studies involve a complex neuromuscular control system that is still in the early stages of investigation. Superficial similarities between modes are likely to be the result of convergent evolution (and generally, underwater modes are not used for terrestrial locomotion), but these similarities may suggest that there are some latent neuromuscular control patterns that would have been present in the common ancestor of fishes and tetrapods.

Conclusions
A large number of diverse fishes are able to move over land using several possible modes of locomotion. The dramatically different force environments that exist on land compared with water dictate how fish use and control their bodies to move in a terrestrial world. Establishing a classification system for describing fish terrestrial locomotion is important for objective comparative studies of fish terrestrial locomotor diversity. Variation in performance metrics such as behaviour, anatomy and activity level are critically linked to body form. Both phylogenetic inertia and basic physical constraints appear to influence the evolutionary patterns of terrestrial locomotion in fishes to support the following conclusions.

Terrestrial fish coopt existing body forms
Preferred modes of locomotion in terrestrial fishes appear to be related primarily to general body shape and secondarily to evolutionary specialization. Only a handful of fish species have evolved overly specialized musculoskeletal systems for terrestrial locomotion. The majority use relatively unspecialized elongate bodies with good terrestrial stability, adequate flexibility and low body mass. This occurs across a diversity of fish clades on the fish evolutionary tree, suggesting limited phylogenetic constraint. Where phylogeny appears to impact terrestrial performance is in the jumping fishes, who are specious but predominantly confined to

a few closely related genera. This diversity suggests a very successful terrestrial strategy amongst jumping fish, something that is represented by an increased effective performance and distance compared with other locomotory behaviours.

Physical constraints drive performance

Successful terrestrial locomotion requires producing effective ground reaction forces to lift one's mass off the substrate and move forward. Both the size and shape of a fish will influence its ability to produce the forces required to accomplish this task. The capacity of tissues to produce and tolerate forces between environments is critical for success. In addition, anatomical specializations, although rare, help facilitate force production and terrestrial locomotor performance. Finally, tissue plasticity, a characteristic of biological tissues, is beneficial in allowing tissues to ameliorate their performance in novel force environments. The innate plasticity of muscle and bone as well as other physiological systems appears both integral and critical to the success of those amphibious fishes studied. An intricate interchange of physical constraint, tissue plasticity and phylogenetic inertia determine the success of terrestrial locomotion across the actinopterygian tree.

Neuromuscular control and plasticity

Fish appear to be able to utilize existing swimming control patterns, modified aquatic escape responses or novel motor control patterns to move overland successfully. The number and phylogenetic distribution of tetrapod-like walking behaviours that have evolved both above and below the water suggest that fish share a common ancestral neural control pattern with tetrapods that drives their locomotor abilities. Of course, without complex neuroethology studies, it is difficult to determine the character and possible origins of neural control patterns in fishes.

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