A comparative analysis of the novel terrestrial locomotion of the tidepool sculpin, *Oligocottus maculosus*

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Abstract

Tidepool sculpins (*Oligocottus maculosus*) are intertidal fish that use a novel mode of terrestrial locomotion to traverse their semi-terrestrial environment. Our goals were to describe the kinematics of the terrestrial locomotion of *O. maculosus* and compare their terrestrial locomotion to their aquatic locomotion, the terrestrial locomotion of subtidal sculpin species (*Leptocottus armatus* and *Icelinus borealis*), and the terrestrial locomotion of walking catfish (*Clarias* spp.). We used high-speed video to record locomotion on a terrestrial platforms and in water, and landmark tracking software in MATLAB to analyze their locomotion. *O. maculosus* use a novel form of axial-appendage-based locomotion, driven by lateral oscillations of the tail synchronized with alternating rotation about the base of their pectoral fins, described as an "army crawl". Unlike *Clarias* spp., which use a diagonal gait, *O. maculosus* use a lateral gait. The army crawl likely originates from a modified series of aquatic fast starts in a terrestrial environment. However, they use axial undulation of the body during aquatic locomotion, whereas they use axial oscillation and pectoral fins in terrestrial locomotion. The army crawl is more effective at moving linearly on land than the terrestrial "wiggle" used by subtidal sculpins. It is possible that the earliest vertebrates on land used forms of terrestrial locomotion analogous to the terrestrial locomotion of fishes. Actinopterygians like *O. maculosus* may have begun the transition onto land before the rise and terrestrial success of sarcopterygians by using behavioral adaptions, which would not show in the fossil record like morphological adaptations.

Introduction

The cyclic process of emersion and immersion in the intertidal zone can often strand organisms on land or in isolated, poorly-oxygenated pools. Many of the organisms in the upper intertidal zone, such as crabs and snails, have adapted to survive periods of desiccation, extract oxygen from the air, and move overland. However, this environment creates an additional challenge for fish (Bressman et al., accepted 2015; Martin and Bridges, 1999; Taylor et al., 2008), which lack an external carapace or shell, and must remain moist to survive. Yet, some fishes have adapted to live in tidepools, including Atlantic mummichogs, *Fundulus heteroclitus* (Bressman et al., forthcoming), and North Pacific sculpins (members of the Cottodei). Both *Fundulus* spp. and intertidal sculpins are hypoxia tolerant (Martin and Bridges, 1999; Martin, 1991; Mandic et al., 2009), and *Fundulus* spp. and some sculpin species can respire on land through their skin (Martin and Bridges, 1999; Martin, 1991; Knope and Scales, 2013), which allows them to extract oxygen from the air cutaneously.

The tidepool sculpin, *Oligocottus maculosus*, is able to home to a tide pool that it has been removed from in the water (Green, 1971), and may be also be able to return to the same tide pool, or to the nearest body of water when on land to avoid dessication, similarly to *F. heteroclitus* (Bressman et al., forthcoming). The tidepool sculpin, *Oligocottus maculosus*, is able to home to a tide pool that it has been removed from in the water (Green, 1971), and may be also be able to return to the same tide pool, or to the nearest body of water when on land to avoid dessication, similarly to *F. heteroclitus* (Bressman et al., forthcoming). However, unlike *F. heteroclitus*, who use burst, periodic locomotion (tail-flip jump; Bressman et al., forthcoming; Gibb et al., 2011; Gibb et al., 2013) on land, *O. maculosus* appear to employ sustained periodic locomotor behaviors

(Alice C. Gibb, pers. obs.), although the body movements that produce this behavior have not yet been described.

Sustained periodic terrestrial locomotion in fishes can be achieved using the axial body, paired appendages, or a combination of the axial body and paired appendages (also termed axial-appendage based locomotion, *sensu* Pace and Gibb, 2014). Axial-based locomotion, such as that found in the ropefish, *Erpetoichthys calabaricus*, involves undulating an elongate body to produce axial undulations that move fish around on land in a manner similar to snakes (Pace and Gibb, 2014). However, *O. maculosus* do not have elongate bodies, so it is unlikely they can effectively move on land *via* this method. Appendage-based locomotion, such as seen in *Periophthalmus* spp., involves highly-modified radials of the pectoral fins that protrude from the body, that enable the fish to “crutch” along the substrate (Pace and Gibb, 2014) with synchronous pectoral fin movements. This is thought to be an uncommon form of locomotion, and *O. maculosus* do not appear to have the required modifications of the radials (Noah R. Bressman pers. obs.). Thus, we hypothesize that *O. maculosus* use the third method of sustained periodic terrestrial locomotion: axial-appendage based locomotion. Fishes that use this method, such as the walking catfishes, *Clarias* spp., coordinate side-to-side whole-body movements with alternating appendage (pectoral fin) movements (Pace and Gibb, 2014).

Due to different physical constraints in an aquatic environment, which is dominated by viscous forces, and a terrestrial environment, which is dominated by gravitational forces, fishes may use different parts of their body for locomotion on land and in water (Pace and Gibb, 2009). For example, *Periophthalmus* almost entirely use their pectoral fins for sustained terrestrial locomotion on land, whereas in water they mostly use their body — typically only using pectoral rowing in conjunction with their bodies at slower speeds (Pace and Gibb, 2009). *O. maculosus* may also use different regions of their bodies in distinct locomotor patterns, depending on the environment.

The goals of this study are to (1) describe the kinematics of the sustained periodic terrestrial locomotion of the tidepool sculpin, *Oligocottus maculosus*; (2) compare the kinematics (body and fin movements) during terrestrial locomotion in *O. maculosus* with their aquatic locomotion; and (3) compare the kinematics (body and fin movements) during terrestrial locomotion in *O. maculosus* with the terrestrial movements of a generally subtidal sculpin species, the Pacific staghorn sculpin, *Leptocottus armatus*, and a fully subtidal species, the northern sculpin, *Icelinus borealis*. Based on the anatomy and ecology of these species, we test the following specific hypotheses.

(1) *O. maculosus* employ an axial-appendage-based terrestrial locomotion, similar to that of *Clarias* spp., and that they are more effective (defined as ability to displace the center of mass across the substrate) at moving over land, relative to *L armatus* and *I. borealis*.

(2) *O. maculosus* use transverse (traveling) waves of axial bending down their body when swimming underwater, whereas they use a standing wave of axial bending when moving on land.

(3) Pectoral fins and the axial body both move in a cyclic pattern during terrestrial locomotion in *O. maculosus,* whereas only the axial body moves in a cyclic pattern during aquatic locomotion.

Materials and Methods

Animals

O. maculosus and *L. armatus* were collected by dip nets from tide pools at Deadman's Bay, San Juan Island, Washington and by seining at Jackson Beach, San Juan Island, Washington. ($n_{\text{tide pool}}$ = ~50; n_{staghorn} = ~10). *I. borealis* were collected via bottom trawls conducted around Orcas Island, Washington. All sculpins studied were approximately the same length (SL = 4.5-8 cm). All experimental animals were housed in flow-through sea-tables at Friday Harbor Laboratories with ambient lighting and an approximate water temperature of 11°C. Fish were fed a diet of live mysid shrimp twice each week. All experiments and procedures were conducted in accordance with UW IACUC protocol #4238-03.

Data Collection and Analysis

Sculpins (n = 6 per species) were individually placed on a damp terrestrial platform (a piece of acrylic covered with a moist paper towel) positioned within a glass aquarium during the locomotor trials. One end of the platform provided access to water, which may serve as incentive for the fish to move across the experimental arena. High-speed video (210 fps) was recorded with two Casio Elixim FH-20 cameras that recorded images simultaneous from above the tank (a dorsal view of the fish) and from the side (a lateral view of the fish). In the terrestrial trials, the sculpins were allowed to move voluntarily without human stimulation or intervention. If a sculpin did not move for over 10 minutes on the terrestrial platform for any trials, it was not included in the analysis. Using the same aquarium and platform as used for terrestrial trials of *O. maculosus*, the terrestrial behaviors of *L. armatus* and *I. borealis* were also recorded using a Casio Elixim FH-20 recording images from an overhead view. The same individuals of *O.*

maculosus used for terrestrial trials were also filmed swimming in water so that we could compare terrestrial locomotor movements with aquatic locomotor movements. For aquatic locomotor trials, the terrestrial platform was removed from the glass aquarium, which was then filled with seawater to a depth of approximately 7.5 cm. If a fish would not swim voluntarily, swimming was initiated by either tapping on the outside of the aquarium or by chasing the fish with a net. The high-speed videos were used to quantify the kinematics of locomotor behaviors. From the terrestrial trials, seven points on the *O. maculosus* were manually tracked using the videos from above (using a digital image analysis program written by Ty Hedrick of the University of North Carolina at Chapel Hill) in MATLAB: (1) tip of snout (2) caudal peduncle (3) center of mass (COM, see below) (4) tip of left pectoral fin (5) base of left pectoral fin (6) tip of right pectoral fin (7) base of right pectoral fin. For the sculpins from the lower intertidal and subtidal, *L. armatus* and *I. borealis*, no pectoral fin movement were observed during terrestrial locomotion, so only points 1, 2, and 3 were tracked for these two species. The approximate location of the center of mass for each species was determined by balancing three dead sculpins on the edge of a sheet of acrylic to the point where they would freely balance, which was deemed the center of mass along the anterior-posterior axis. The tip of snout was defined as the most anterior point on the fish. The caudal peduncle was defined as the base of the caudal fin rays. The tips of the pectoral fins were defined as the most distal point on each fin. The bases of the pectoral fins were defined as the insertions of the pectoral fins.

For all points measured for all species, displacement versus time was plotted to determine movement of various regions of each fish. Wave amplitudes (as defined as the maximum amplitude of the head, COM, and caudal peduncle in terms of % body length as standard length (SL)), curvature coefficients (a ratio of the distance between the snout and peduncle when the tail is at the maximum amplitude – as defined as maximum curvature of the caudal peduncle – to the SL, modified from Brainerd and Patek (1998)), and stride frequencies were also measured using MATLAB and ImageJ. The purpose of the curvature coefficients is to measure how far anteriorly the fishes move their tails. The purpose of the wave amplitudes is to measure how far laterally the snout, COM, and peduncle move during strides. The stride frequency is a measure of how rapidly the fishes move their tails laterally. Similar to the stride definition by Ashley-Ross and Lauter (1997), a single stride was defined as the lateral movement of the caudal peduncle from maximum curvature to the maximum curvature again on the same side of the body.

For the three sculpin species, a "distance ratio" was calculated for the snout, peduncle, and COM. The distance ratio is a measure of the sinuosity of movement and defined as the net displacement of the points over a series of full strides divided by the gross displacement (Pace and Gibb, 2014). The purpose of the distance ratio is to determine the effectiveness with which each species moves linearly. In order to determine whether standing or transverse waves are employed in locomotion on land or in water, the maxima of the waves at different points along the body were analyzed in MATLAB.

Results

O. maculosus employ a previously undescribed form of axial-appendage-based locomotion. Starting while resting on its ventral surface with a bend in the axial body and the pectoral fin on the inside of the curve held up against the body (abducted), a tidepool sculpin will draw its pectoral fin towards its body and move the tail towards its midline, beginning a stride. The fish will continue swinging its tail across the midline and toward the opposite (contralateral) side of the body. As the fish is swinging the tail through the first half-stride, the fish will place the contralateral pectoral fin in direct contact with the substrate. The fish then rolls partially around its long axis, towards the stationary pectoral fin and also strikes the substrate with the caudal peduncle as the tail crosses the midline. Contact with the ground at the peduncle and the pectoral fin allows the fish to drive the central region of the axial body vertically, up and off the substrate. Pushing off the substrate with its tail while arching its body off of the substrate allows the sculpin to rotate the central body, including the center of mass, about the base of the stationary pectoral fin. The body will rotate until the pectoral fin is fully abducted from the body and the tail has swung in an arc to the opposite side of the body, and then the sculpin will repeat this series of movements, swinging the tail back to the original side and placing the opposite (contralateral) side pectoral fin to produce the second half-stride of the tail. *O. maculosus* move in an overall, anteriorly-directed, linear fashion, in a behavior we describe as an “army crawl,” as it appears to mimic the “leopard crawl” of human military personnel (Noah R. Bressman pers. obs.; Fig. 1). In order to change the direction movement, a sculpin will increase the amplitude of the tail on one side to increase rotation towards the other side. The sculpin will then either move in a roughly straight line or use another increased amplitude tail movement on the same side to continue changing direction. *O. maculosus* move their tail on land with an average frequency of

9.9 Hz (Fig. 1). They have a terrestrial velocity of 1.6 BL/s (SL is used as a body length; Fig. 2).

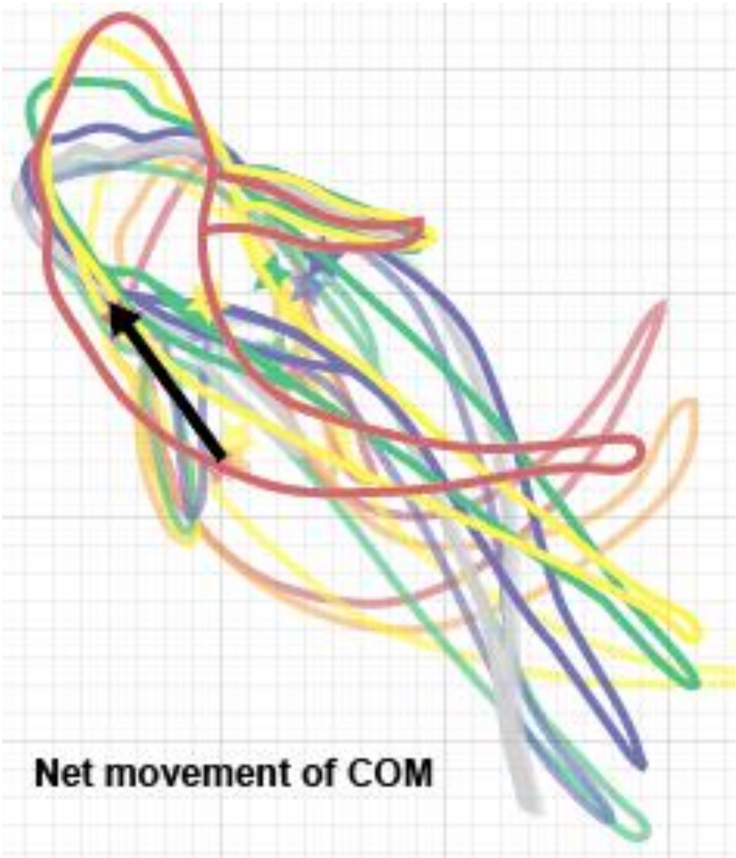

Figure 1. Outline of a stride by *O. maculosus*. In this series of outlines of an army crawl stride, it can clearly be seen that *O. maculosus* rotate their bodies around alternatingly fixed pectoral fins. Stars indicate the location of the COM throughout the stride.

L. armatus, the sculpin typically found in the shallow subtidal and low intertidal, employs a similar caudal and posterior body movements as the tidepool sculpins, but does not use cyclic motions of the pectoral fins and achieves very little anteriorly-directed movement of the COM. We term this behavior a “wiggle”. While lying on its ventral surface, a staghorn sculpin will oscillate its tail laterally from side-to-side with a larger amplitude than tidepool sculpins (Fig. 4a). When a *L. armatus* moves its tail to one side, it also moves its head to the same side, bending around the COM. *L. armatus* move their tail on land with an average frequency of 7.0 Hz (Fig 2). They have a terrestrial velocity of 0.5 BL/s (Fig. 3).

Similarly to *L. armatus*, *I. borealis* oscillate the body from side to side, but produce little anterior movement. When stranded on land, an individual of *I. borealis* will move the tail laterally towards its head. As the caudal peduncle approaches the head during a tail half-stride, *I. borealis* will move its head laterally, towards its tail, until the side of the snout is in direct contact with the caudal peduncle, thereby forming a circle with the body. It then repeats this movement by oscillating the tail in a second half-stride toward the opposite side. While sometimes *I. borealis* will oscillate the tail at roughly a constant speed, occasionally they will move their tail more slowly towards one side, and then, as the tail approaches maximum curvature, the fish will rapidly accelerate its caudal peduncle and head towards each other in what we term a “jamming” motion. We are describing this behavior as a “tail-jam wiggle”. During a tail-jam wiggle, the center of the body remains in full contact with the substrate, but the head and tail may lift off the substrate. *I. borealis* move their tail on land with an average frequency of 13.6 Hz (Fig 2). They have a terrestrial velocity of 0.4 BL/s (Fig. 3). In a typical tail-jam wiggle, *I. borealis* does not achieve any significant rotation or linear displacement of the COM. However, if its body and tail rotate during the tail-jam wiggle so that the lateral side makes contact with the substrate, it will use the same motion as the tail-jam wiggle, but launch itself into the air and flip tail-over-head or roll tail-over-head into a “summersault”.

When moving in water, *O. maculosus* produce cyclic swiming by passing transverse (traveling) waves down the posterior of their body. They typically swim in series of small, successive bursts of a few strides each, rather than steady swimming. To initiate swimming while at rest on the substrate, *O. maculosus* rotate their body about the base of their pectoral fin on the same side that the tail is bent toward. Then they rapidly adduct both pectoral fins, with the adduction initiated on the side of axial bending, and initiate an aquatic fast start. To continue swimming, their pectoral fins will be partially abducted while they cyclically undulate the axial body and tail fin. While swimming at higher speeds, *O. maculosus* will fully adduct their pectoral fins. When they stop swimming, they will fully abduct their pectoral fins to brake. During steady swimming, they move their tail with a frequency of 15.4 Hz, but they can achieve a stride frequency of 27.4 Hz (Fig.2).

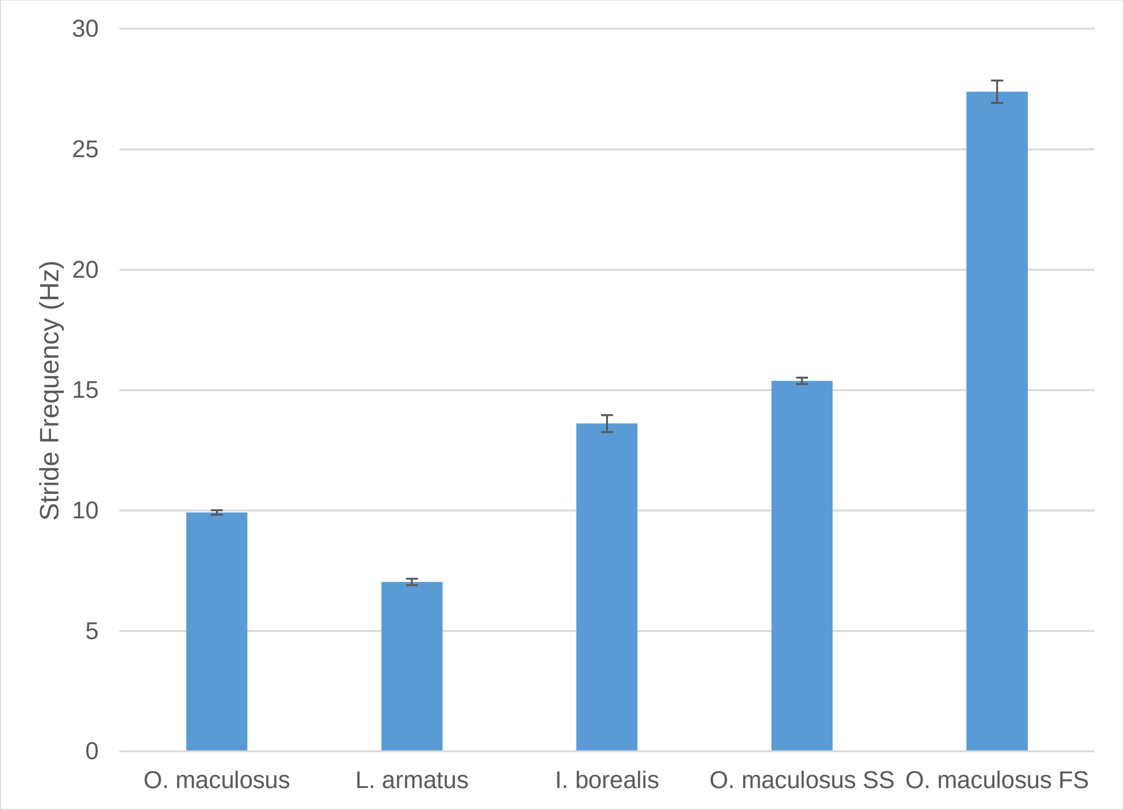

Figure 2. Average stride frequencies (Hz). In addition to the three sculpin species recorded on land, the stride frequencies of the *O. maculosus* during steady swimming (SS) and fast swimming (FS) are included in this figure.

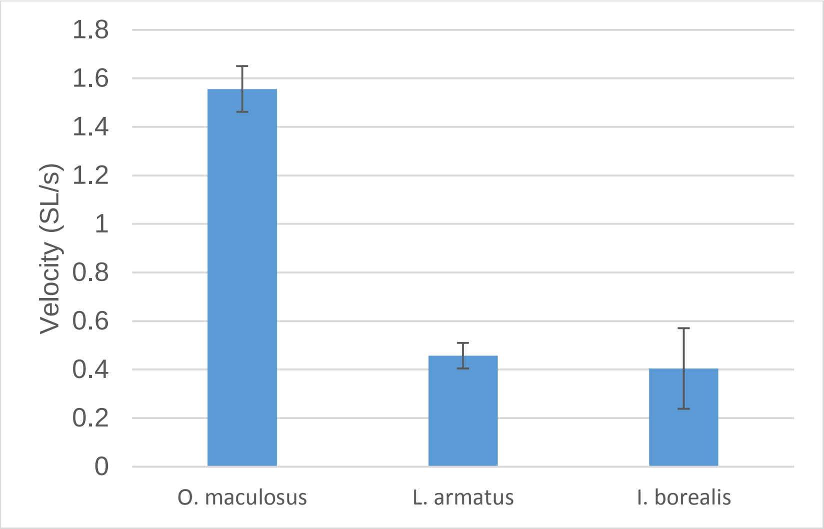

Figure 23. Terrestrial velocity of three sculpin species in body lengths (as SL) per second.

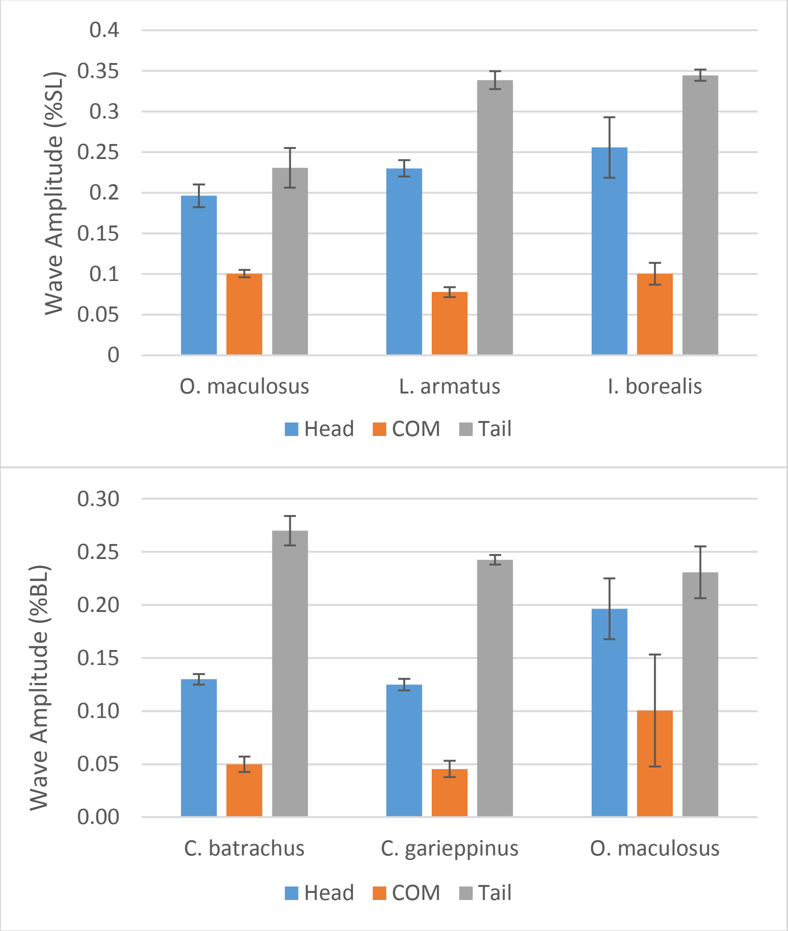

Figure 4. Wave amplitudes of sculpins and amphibious fish. The wave amplitudes for the snout (head), COM, and caudal peduncle (tail), as %SL, are shown for the three sculpin species in Fig. 4a. The wave amplitudes of *O. maculosus* and two other species of fish that use axial-appendage-based terrestrial locomotion, the Asian walking catfish, *Clarias batrachus*, and the African walking catfish, *C. gariepinus*, are shown in Fig. 4b as % body length (BL).

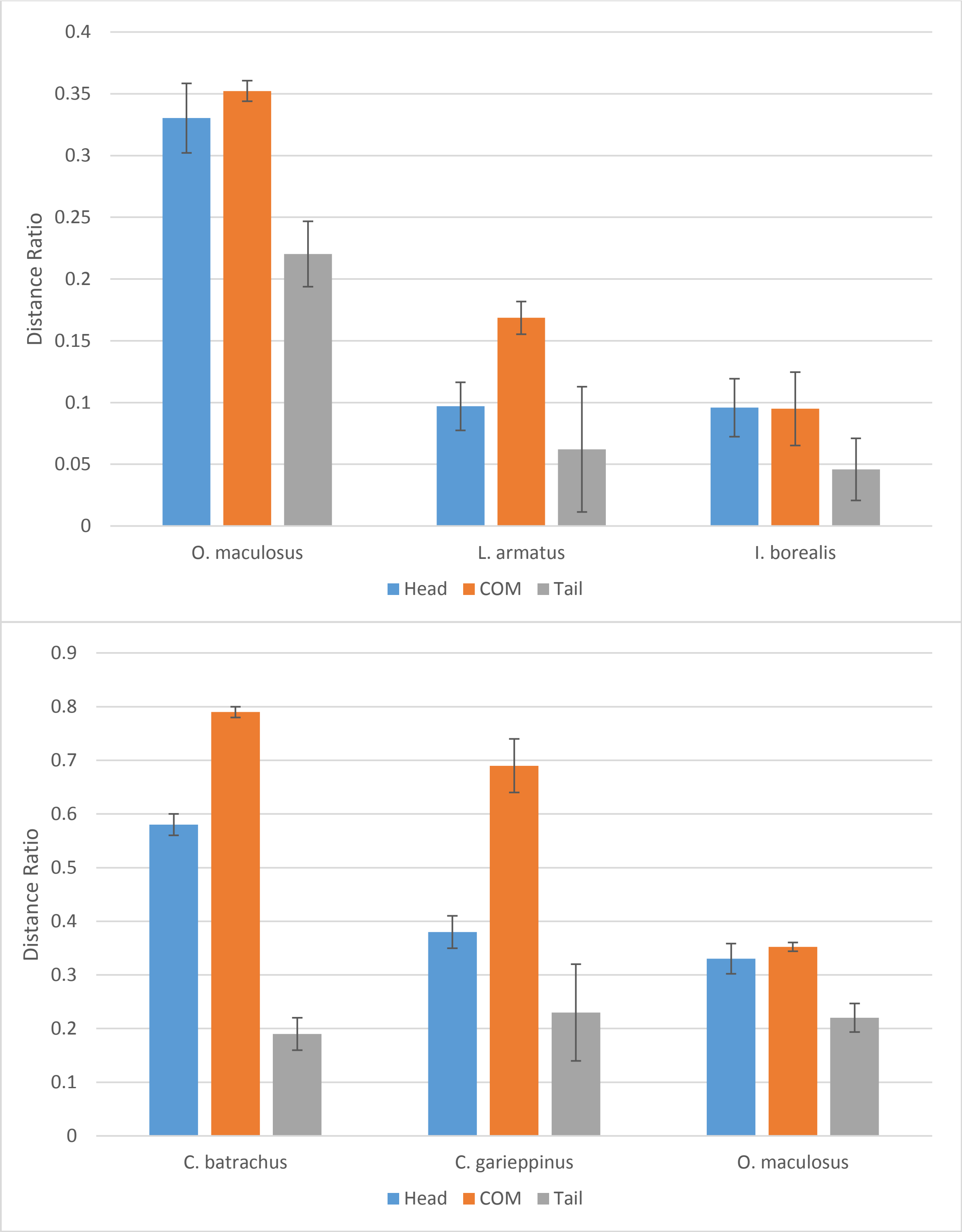

Figure 5. Distance ratios of sculpins and amphibious fish. The distance ratios for the head, COM, and tail, are shown for three sculpin species in Fig. 5a. The wave amplitudes of *O. maculosus*, *C. batrachus*, and *C. gariepinus*, are shown in Fig. 5b.

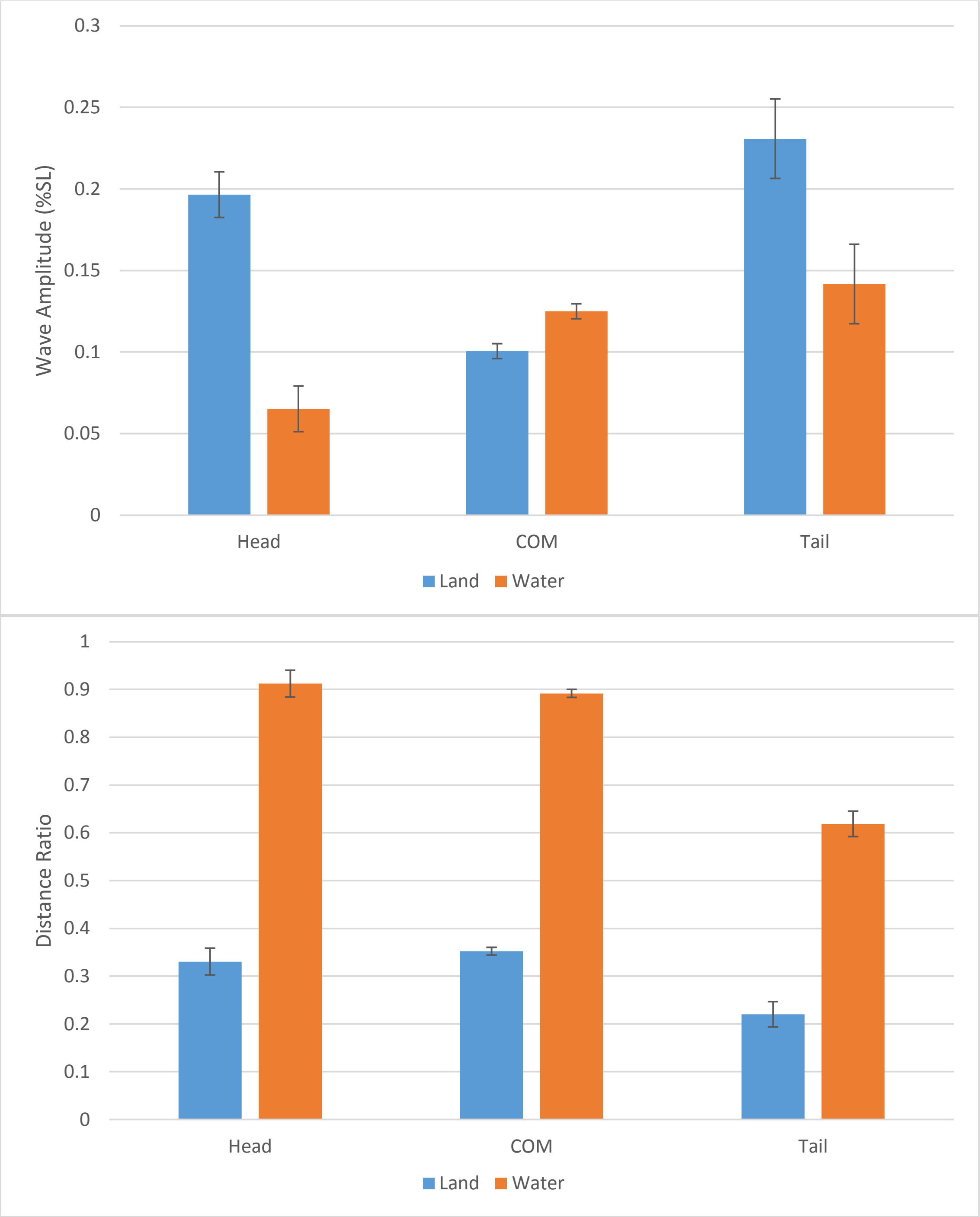

Figure 6. Aquatic vs. terrestrial locomotion of *O. maculosus*. Wave amplitudes (6a) and distances ratios (6b) for the head, COM, and tail are compared between *O. maculosus* locomotion in terrestrial and aquatic environments

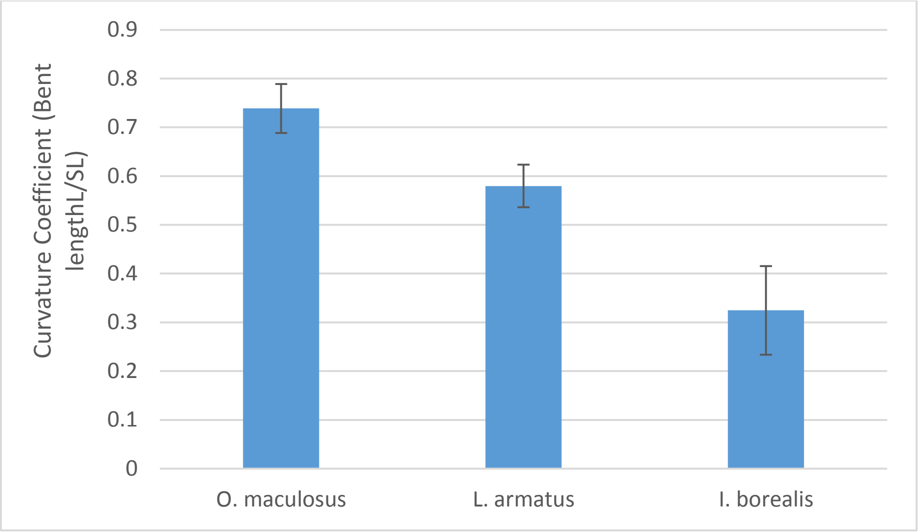

Figure 7. Terrestrial curvature coefficients.

Discussion

Based on tail wave amplitude (Fig. 4a), distance ratios (Fig. 5a), curvature coefficients (Fig. 7), velocity *O. maculosus* are more effective at moving over land than *L. armatus* or *I. borealis*. *O. maculosus* move over land more quickly, in a more linear path, and with less tail movement than the other two species. This means that in the wild, they would be expected to be able to return to water more quickly when stranded to avoid predation, desiccation, and suffocation.

Tidepool sculpins have a similar behavior to that of walking catfish. The wave amplitudes and the tail and snout distance ratios of the *O. maculosus* are very similar to that of the two walking catfish species studied by Pace and Gibb (2014), particularly of the African walking catfish, *Clarias gariepinus* (Fig. 4b, 5b). However, the COM distance ratio is much greater for *Clarias* spp. than *O. maculosus*. This could be because they employ different types of axial-appendage-based terrestrial locomotion. A *Clarias* spp. has its tail and pectoral fins 180° out of phase – meaning that when the tail is in contact with the substratum on the left, the right pectoral fin is in contact with the ground

(Pace and Gibb, 2014) – with a similar diagonal walking gait to that of many tetrapods (Hildebrand, 1980). Meanwhile, the *O. maculosus* moves its tail and pectoral fins in phase, so that when the left pectoral fin is extended, the tail is on the left side of the body, similar to the lateral gait, or rack, of giraffes, elephants, and camels (Hildebrand, 1980; Dagg, 1974). By having the fins and tail out of phase, *Clarias* spp. may be able to rotate more efficiently about their COM than the sculpins, accounting for their greater COM distance ratio. *O. maculosus* rotate about the base of their long pectoral fins, whereas *Clarias* spp. rotate around the tips of their pectoral spines (Johnels, 1957; Pace and Gibb, 2014. The COM is farther away from the tip of the pectoral fin than the base. To move their COM the same net distance as *Clarias* spp., *O. maculosus* would have to rotate more radians around the base of their pectoral fins, which can explain why they have a smaller COM distance ratio. While *O. maculosus* do have a lesser distance ratio, their stride frequency of 9.9 Hz is much greater than *Clarias* spp., which move at about 0.5 Hz (Johnels, 1957). As *Clarias* spp. are larger, they may not be able to move with the as high a frequency or velocity (BL/s) as *O. maculosus*.

The “wiggle” of *L. armatus* and *I. borealis* appears to be similar to the “squiggle” behavior of *K. marmoratus* described by Pronko et al. (2013) and to the “wriggle” behavior in mummichogs, as described by Bressman et al. (forthcoming). However, unlike the squiggles, which achieve linear displacement, and the wriggles, which achieve rotational displacement, wiggles achieve little-to-no displacement. On a semi-terrestrial surface, wriggling may create enough force to overcome static friction, allowing them to move more effectively on a film of water. On an incline, wiggling combined with gravity may create enough force to overcome static friction, allowing these fish to move downhill. Summersaults initiated by tail-jam wiggles of *I. borealis* on inclines may also induce tire-like rolling downhill, using a similar concept to the roll by *Gambusia affinis*, but along a different axis (Boumis et al., 2014).

Of the three sculpin species, only *O. maculosus* appears to be effective at locomoting on flat land (zero slope). In terms of kinematics and measurements, *O. maculosus* locomotes more efficiently than *L. armatus* and *I. borealis* in every way, except for COM distance ratios and stride frequencies. *L. armatus* and *I. borealis* likely have greater COM distance ratios than *O. maculosus* because they achieve very little linear motion, rotating back-and-forth about their COM. *L. armatus* have a lower stride frequency than *O. maculosus*, likely due to their flattened ventral surface, which could create greater friction, slowing down their wiggling. However, *I. borealis* have a greater stride frequency than *O. maculosus*, which could be because *I. borealis* often lift their head and tail slightly off the ground when wiggling, reducing friction. Regardless, *O. maculosus* are the only of the three sculpin species capable of effectively locomote linearly on a flat, terrestrial surface.

O. maculosus appear to have pectoral fin adaptions that allow them to perform better on land than *L. armatus*. *O. maculosus* have longer pectoral fins with less webbing on the ventral surface than *L. armatus*, which allows them to better grip the substrate with their fins (Kane, 2012) during terrestrial locomotion. *O. maculosus* also have smaller pectoral fins insertions than *L. armatus* (Kane, 2012), so they have more freedom of rotation in their pectoral fins, allowing them to better rotate around their fins during terrestrial locomotion. These adaptations for terrestrial locomotion are useful for *O. maculosus*, as they live in unstable, ephemeral tide pools, whereas subtidal sculpins likely did not evolve these adaptions, as they may not be useful in a subtidal environment. Even though *I. borealis* have similar morphologies to *O. maculosus*, they are not capable of army crawling, suggesting there is more involved in terrestrial locomotion than morphology. The adaptations of *O. maculosus* for terrestrial locomotion are useful to them, as they live in unstable, ephemeral tide pools. Subtidal sculpins likely did not evolve these morphological and behavioral adaptions, as they may not be useful in a subtidal environment.

There are fundamental differences between the aquatic and terrestrial locomotion of *O. maculosus*. In water, they undulate their bodies, sending transverse waves posteriorly through their body, as seen by the increasing wave amplitude from head to head (Fig. 6a). On land, they oscillate their body in standing waves, with greatest amplitude at the head and tail (Fig. 5a). Pectoral fins are used for braking steering, and propulsion during acceleration when swimming, whereas on land, they are used as pivots and do not provide propulsion. As their bodies are primarily design for life in water, they can move much more quickly and more effectively in water (Fig. 6b).

However, there are also some similarities between the kinematics of the terrestrial and aquatic locomotion of *O. maculosus*. Their army crawl and aquatic fast starts have similar tail and pectoral fin synchronizations and amplitudes, and they rotate about their pectoral fin during both forms of locomotion, except the extent to which they rotate is greater on land. It appears that the kinematic origin of the *O. maculosus* army crawl is their aquatic fast start, which they have adapted to create a form terrestrial locomotion. An army crawl is essentially a series of aquatic fast starts to alternating sides in rapid succession on land.

Terrestrial locomotion in fishes is a great analog for how vertebrate life transitioned from water to land in terms of locomotion. Some early tetrapodamorphs, like *Icthyostega*, are thought to have used modes of terrestrial locomotion similar to the appendage-based crutching of *Periophthalmus* spp. (Pierce et al., 2014). As newer fossil evidence is discovered, pushing the origin of the first tetrapods on land further back (Niedźwiedzki, 2010), it becomes more likely that the earliest vertebrates on land, be it tetrapod, fishapod, or fish, used forms of terrestrial locomotion analogous to the terrestrial locomotion of fishes. Actinopterygians like *O. maculosus* may have begun the transition onto land before the rise and terrestrial success of sarcopterygians using behavioral adaptions, which would not show in the fossil record like morphological adaptations.

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