

A novel intramandibular joint facilitates feeding versatility in the sixbar *distichodus*

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Summary statement:

The sixbar *distichodus* is a freshwater, plant-eating fish with an extra joint in its lower jaw that allows it to feed in new ways compared to fishes lacking the joint.

ABSTRACT

The intramandibular joint (IMJ) is a secondary point of movement between the two major bones of the lower jaw. It has independently evolved in several groups of teleost fishes, each time representing a departure from related species in which the mandible functions as a single structure rotating only at the quadratomandibular joint (QMJ). In this study, we examine kinematic consequences of the IMJ novelty in a freshwater characiform fish, the herbivorous *Distichodus sexfasciatus*. We combine traditional kinematic approaches with trajectory-based analysis of motion shapes to compare patterns of prey capture movements during substrate biting, the fish's native feeding mode, and suction of prey from the water column. We find that the IMJ enables complex jaw motions and contributes to feeding versatility by allowing the fish to modulate its kinematics in response to different prey and to various scenarios of jaw-substrate interaction. Implications of the IMJ include context-dependent movements of lower versus upper

jaws, enhanced lower jaw protrusion, and the ability to maintain contact between the teeth and substrate throughout the jaw closing or biting phase of the motion. The IMJ in *D. sexfasciatus* appears to be an adaptation for removing attached benthic prey, consistent with its function in other groups that have evolved the joint. This study builds on our understanding of the role of the IMJ during prey capture and provides insights into broader implications of the innovative trait.

INTRODUCTION

Although suction is the dominant mode of prey capture found across teleost fishes, many species feed by directly biting prey that are attached to a substrate. Suction is a highly versatile mechanism for overcoming the escape responses of free-moving, midwater prey but may not exert sufficient forces to remove many potential prey that are anchored by holdfasts or other gripping mechanisms. Fishes that feed by biting attached food from benthic substrates are able to take a wide range of otherwise inaccessible prey, like plants, algae, sponges, corals, and other anchored invertebrates (Jones, 1968; Bellwood and Choat, 1990; Ferry-Graham et al. 2012). A defining characteristic of this feeding mode is the direct interaction between a fish's jaws and its food, which is integral to prey acquisition and not secondary or incidental as in suction feeders (Corn et al., 2021). Of potential importance is the variability introduced by the substrate itself, which is rarely uniform, varying widely in topology, orientation, and rugosity. Therefore, an ability of the jaw system to modulate its movements in response to the feeding surface is likely important for removing attached prey in structurally diverse benthic habitats (Lujan and Armbruster, 2012; Bellwood et al., 2014).

Adaptations displayed by benthic biting fishes include force-modified jaws with greater stability across joints (Alfaro et al., 2001), coupled with specialized dentition for scraping, picking, shearing, and gouging (Bellwood and Choat, 1990; Streelman et al., 2003; Albertson and Kocher, 2006; Streit et al., 2015). Still, the feeding mechanisms of a vast majority of biting fishes are limited in their capacity to remove attached prey in at least two important ways. First, a consequence of having short, force-modified jaws is that gape size is reduced and so is the area across a food-bearing surface that can be swept by the teeth (Gibb et al., 2015). Second, the lower jaw of most teleost fishes functions as a single structure with one point of rotation at the quadratomandibular joint, QMJ (Fig. 1A), so movements of the teeth on a substrate are

constrained along a distinct arc-shaped path. This limits the ability of teeth to maintain contact with most benthic surfaces without supplemental movements of the body (Konow et al., 2008). One of the ways that fishes feeding on attached prey have dealt with these challenges is the evolution of an intramandibular joint (IMJ), an extra point of flexibility that allows independent mobility between the two primary bones of the lower jaw, the angulo-articular (articular, hereafter) and tooth-bearing dentary (Fig. 1B). The IMJ appears to have evolved at least ten times across teleost fishes and is always associated with a benthic biting feeding mode (Purcell and Bellwood, 1993; Bellwood, 1994; Konow et al., 2008; Ferry-Graham and Konow, 2010; Gibb et al., 2015).

While the IMJ may represent a convergent trait for accessing a specific class of prey, there is substantial functional variation of jaw systems across different groups possessing the novelty (Konow and Bellwood, 2005; Konow et al., 2008; Ferry-Graham and Konow, 2010; Konow and Bellwood, 2011; Ferry et al., 2012; Gibb et al., 2015). A likely reason is that the IMJ adds a degree of freedom to the lower jaw system compared to traditional single-structure mandibles, opening a new landscape of morphological and kinematic solutions not possible otherwise (Vermeij 1973). And when there are new ways to be kinematically diverse, there are more options for solving functional problems. We therefore expect fishes possessing an IMJ to use the added flexibility for enhanced kinematic versatility, the ability to modulate movement patterns under different scenarios. The most recognizable form of versatility is patterned variation for *divergent* performance outcomes, like employing different feeding modes (Liem 1980) or swimming behaviors (Drucker and Lauder 2003), in which each task is achieved through a distinct and predictable pattern of movement. However, kinematic versatility can also be expressed as an ability to modulate movements for a *single* performance outcome. For example, some algae-eating catfishes are thought to accommodate interactions with the substrate through differential movements of left and right mandibles, allowing a scraping motion of the jaws to proceed despite uneven surfaces (Adriaens et al., 2009). While the first example impacts the mean kinematic pattern (different motions for different tasks), the latter is likely to impact kinematic variance (greater modulation for tasks involving response to an external factor).

Here, we examine the function of the IMJ and its influence on feeding kinematics, using the sixbar distichodus (*Distichodus sexfasciatus* Boulenger 1897) as a case study. *D. sexfasciatus* is a freshwater fish found primarily in the Congo River basin and in Lake Tanganyika (Arroyave

et al., 2020). The presence of the IMJ novelty has been documented in many species within the family Distichodontidae but is in its most mobile form in the genera *Distichodus* and *Nannocharax* (Vari, 1979). Like several other fishes with IMJs, species within *Distichodus* are broadly classified as herbivores (Lavoué et al., 2017). Detailed dietary studies in a number of species show that while macrophytes are the dominant dietary items, the primary sources of prey are variable and include, leaves, stems, roots, and filamentous algae (Arawomo, 1982; Inyang and Nwani, 2004; Berté et al., 2008; Mbadu Zebe et al., 2010; Dietoa et al., 2014). There is also documented variation in diets between the wet and dry seasons, presumably because of temporal differences in relative prey abundance (Inyang and Nwani 2004; Mbadu Zebe et al., 2010).

This study explores morphological and functional details of the IMJ novelty in *D. sexfasciatus* and seeks to understand its role in producing a kinematically versatile feeding system, as defined above. We use an experimental setup that includes examination of movements during both substrate biting and suction-feeding in the water column. The inclusion of suction, despite apparently being of secondary importance in nature, provides a contrast to biting-based motions in which kinematic variation due to interactions with the substrate would be absent. We used a traditional kinematic approach, tracking anatomical landmarks through time to understand the basic sequence of movements during prey capture in *D. sexfasciatus*. From these landmarks, we also computed two kinematic traits, lower jaw protrusion and a ratio comparing upper versus lower jaw movements, that were designed to illustrate how the IMJ enables the fish to modulate feeding motions. In addition, we implemented a landmark-based method using geometric morphometrics for comparisons of kinematic pattern at the whole-motion level. The combination of these approaches enabled a multifaceted assessment of versatility. We first hypothesized that biting and suction would result in divergent feeding kinematics, consistent with a jaw system capable of producing contrasting performance outcomes for different prey types. Here, we expected that lower jaw protrusion and whole-motion kinematic patterns would differ in their mean values between feeding modes. Our second hypothesis was that feeding mode would impact kinematic variance. We expected the jaw movement ratio and whole-motion kinematic patterns to be more variable for biting movements due to IMJ-facilitated modulation, in this case for maintaining a single performance outcome (i.e., the acquisition of attached prey along a flat benthic surface) under various scenarios of jaw-substrate interaction. Lastly, we combine observations on kinematic variation and a model-based argument to highlight a function often

attributed to IMJ feeding systems, but not explicitly shown, the ability to maintain contact between the jaws and substrate during biting (Gibb et al., 2008; Konow et al., 2008; Ferry et al., 2012).

MATERIALS AND METHODS

Oral Jaw Morphology

We examined the cranial morphologies of five preserved *D. sexfasciatus* specimens using one of two preparation methods. Three individuals were cleared and double stained based on a modified protocol by Potthoff (1984) to visualize bone and cartilage in a manner that preserves articulations of skeletal elements. Two additional specimens were stained, but the flesh was not cleared (Springer and Johnson, 2000) and these were then dissected to identify the arrangement of muscles powering the jaw system and their points of attachment to skeletal features. Detailed descriptions of distichodontid morphology by Vari (1979), who followed Winterbottom (1974), were used for myological nomenclature and for guiding morphological assessment.

Feeding Videos

We studied and statistically compared feeding kinematics in five wild-caught fish that were purchased through the aquarium trade. Individuals ranged in size from 8.3 cm – 15.2 cm TL and were housed individually in 30-gallon aquaria where they acclimated for a minimum of one week prior to filming. All care and filming of fish was conducted under UC Davis IACUC protocol 20475.

Individuals were offered two diet items to elicit contrasting feeding modes. Small black worms, *Lumbriculus sp.*, were added to tanks one-by-one with a pipette for fish to capture by suction feeding in the water column. We also presented fish with an attached benthic prey to induce biting motions. This consisted of a strip of cucumber mesocarp, approximately 4 cm x 1 cm (L x W) and 0.25 cm in thickness. Cucumber strips were secured with rubber bands to a ceramic block that was placed on the bottom of the fish tank so that the food was accessible from a vertically oriented substrate (Fig. S1). For both suction and biting-based feeding events, fish were filmed from a lateral view at 2,000 frames per second with a high-speed camera. In total, 64

feeding motions were captured, including 22 biting strikes (n=5, 7, and 10 feeding events across three individuals) and 42 suction strikes (n=2, 9, 10, 10, and 11 events across five individuals).

Kinematic Data and Statistical Comparisons

From each video, 19 frames were used to represent a feeding motion. The first frame was the initiation of the feeding movement, the tenth frame was full gape, and the final frame was full retraction of the jaws to a closed-mouth state. Eight frames were sampled equally through time from start to peak gape for the opening phase of the feeding motion, and another eight between peak gape and the final frame for the closing phase. On each video frame, we digitized twelve fixed landmarks on the head and jaws to capture feeding-associated movements (Fig. S2). Subsequent processing of landmark data (“unaligned shape data”, hereafter) varied depending on the particular aspect of feeding kinematics examined.

A primary goal of this research was to study versatility by contrasting prey capture kinematics (i.e., trait means and variances) between biting and suction-based feeding modes. Whenever possible, we combined data for all individuals measured. However, we were mindful of the possibility that kinematic differences among individual fish could confound comparisons of feeding modes. Therefore, in each analysis described below, we first tested for differences between individuals (i.e., those with greater than two strikes) within each feeding mode. If neither biting nor suction feeding showed differences across individuals, then we combined them for the analysis in question. If there were statistically significant differences across fish, we compared biting versus suction in separate analyses for each individual with three or more strikes per feeding mode. All statistical analyses described in the following sections were done in the R package *geomorph*, v. 4.0.0 (Adams et al., 2019; R Core team, 2020) based on 10,000 residual randomization permutations through the package *RRPP*, v. 1.0.0 (Collyer and Adams, 2018; Collyer and Adams, 2019). R Code for analyses can be found in archived data (see below).

Kinematic Sequence of Jaw Components

Subsets of landmarks from unaligned shape data were used to examine the kinematic sequence of activation for select morphological features (Fig. S2). Jaw movements of laterally filmed fish were measured in the sagittal plane. Mouth gape was the linear distance between landmarks for the anterior tooth on the upper and lower jaws. Lower jaw bones occur in series (Fig. 1B) and

their directions of movement were measured relative to starting position, using sets of three landmarks. The articular rotates about the base of the lower jaw (the QMJ), and we characterized forward movement away from the head (and towards the prey) as extension and movement back toward the head as flexion. The dentary rotates about the distal end of the articular (at the IMJ) and we used the same terminology to describe movements toward or away from the head. We note that the flexed posture of the lower jaw at rest results in extension at these two joints involving ventral rotation of the articular but dorsal rotation of the dentary. In contrast, the upper jaw is composed of a fused maxilla and premaxilla that rotates as a single structure about the supraethmoid. Its movement is constrained along a simple transcribed arc, not unlike the lower jaw of most teleosts that lack an IMJ (Fig. 1A), and we describe its rotation as either dorsal (mouth opening) and ventral (mouth closing).

Divergent Performance Outcomes: Lower Jaw Protrusion

The rotation of the dentary about the IMJ changes the effective mandible length (EM), the linear distance from the base of the lower jaw (QMJ) to the anteriormost lower jaw tooth (Fig. 1B, dotted line). The ability to adjust the EM has been described as a means of reducing out-lever length for increased mechanical advantage during substrate biting (Ferry-Graham and Konow, 2010), but lengthening of the EM could also be used as a form of lower jaw ram during suction feeding. We measured EM at each stage of the feeding motion and subtracted these values from the starting position to get the amount of lower jaw protrusion attributed to IMJ mobility. Maximum protrusion values were extracted from motions and compared between feeding modes with an ANOVA using the “*procD.lm*” function in *geomorph*. The expectation was that protrusion would be greater for suction feeding than for biting, producing divergent kinematic outcomes in which suction feeding had greater jaw ram and biting was tuned for greater bite force.

Single Performance Outcome: Modulation of Upper and Lower Jaw Movements

Movement of the upper jaw of *D. sexfasciatus* is simple, as described above, rotating about a single proximal point where the upper jaw articulates with the neurocranium. However, the complex movements possible in the IMJ-containing lower jaw may allow for modulation of upper versus lower jaw contributions to gape closure. For instance, if the upper jaw engages with

a benthic substrate, the lower jaw may move in a dorsal direction to close the gape. The reverse is also possible, as is equal movement of upper versus lower jaws. Such variation is expected to be less prevalent for suction of prey from the water column as this feeding mode lacks interaction of the jaws with a feeding surface. We examined the relative movements of upper versus lower jaws during the biting or gape closing phase of feeding motions. To do this, we isolated the anterior tooth landmarks from the unaligned shape data and measured the distance that each traveled from peak gape to tooth occlusion (i.e., the point at which the upper and lower jaw teeth touch prior to retraction of the jaws). We then took the natural logarithm of the ratio of lower jaw to upper jaw movement. A value of zero indicates equal movements of both upper and lower jaws, positive values suggest greater lower jaw movement, and negative values mean greater upper jaw movement. We tested for differences in variance of jaw movement ratios between biting and suction feeding with the “*morphol.disparity*” function in *geomorph*, expecting greater variation for biting strikes as a compensatory response of the feeding mechanism to variation induced by jaw-substrate interactions.

Versatility of Whole-Motion Kinematic Patterns

While individual kinematic traits provide information about movement at specific anatomical loci, we have generally lacked the ability to assess differences in kinematic pattern and diversity at the whole-motion level. Here, we use an application of geometric morphometrics that does just this by characterizing movements as trajectories of shape change (Martinez et al., 2018; Martinez and Wainwright, 2019). Specifically, we start with the abovementioned unaligned shape data (19 head shapes per motion, each defined by 12 cranial landmarks) and align them using generalized Procrustes analysis with the “*gpagen*” function in *geomorph*. Here, each observation (i.e., each subject of alignment) is a cranial shape at a single stage of a feeding motion and the metric of size used in scaling is the centroid size of the head. After alignment, each head shape can be represented as a single point in a high-dimensional morphospace. Different shapes occupy different locations across this space, and the ordered progression of 19 head shapes describing each feeding motion creates a 19-point path or trajectory through the space. Any kinematic variation across the observed motions will impact the relative locations of head shape landmarks and will be reflected in the resulting paths the trajectories take (i.e., the shapes of the trajectories themselves). Before comparing trajectory shapes, a second alignment is needed in which each

observation is now the full collection of cranial landmarks for an entire motion and centroid size of the entire trajectory is the factor used for scaling. We did a trajectory alignment using adapted code from the “*trajectory.analysis*” function in the package *RRPP*. Sources of variation that can impact trajectory shapes include differences in the relative extent and timing of movements of anatomical features (Martinez and Wainwright, 2019). Different kinematic patterns associated with biting and suction feeding modes, if they exist, will therefore result in divergent trajectory path shapes.

Differences in kinematic pattern between feeding modes were examined with comparisons of trajectory shape and variance. We used the “*procD.lm*” function in *geomorph* to do a MANOVA, testing whether mean shapes of biting and suction-based motion trajectories were different as an indicator of divergent kinematic patterns. Next, we did an analysis of kinematic variance between biting and suction feeding strikes with the “*morphol.disparity*” function in *geomorph*. This approach is commonly used to compare dispersion of Procrustes-aligned landmark data for nonmoving morphologies, like interspecific head or body shapes (e.g., Martinez and Sparks, 2017). Here, we apply the method in a new approach for measuring kinematic variance as dispersion of Procrustes-aligned trajectory shapes.

Modeling Jaw-Substrate Interaction

The lower jaw mechanics of *D. sexfasciatus* were modeled as a two-arm lever system to capture rotational movements of the articular and dentary during biting (Fig. 1B). Lever arm lengths (measured at peak gape) and rotational angles used to inform the model were calculated from unaligned shape data for a single observed biting event. We measured total rotation of the articular and dentary over three distinct motion phases, jaw opening (motion initiation to peak gape), biting (peak gape to tooth occlusion), and jaw retraction (closed gape to full retraction of jaws to the head). Next, these angles were divided evenly across motion stages for each phase. For example, the dentary rotated 14.75 degrees over the 10 stages of the opening phase, so rotation between each stage was $14.75/(10-1)$, or 1.64 degrees. This resulted in lower jaw kinematics where rotational movements of lower jaw bones maintained a constant rate of change during each motion phase.

We assembled the model based on a triangle with sides for the articular and dentary, which share a vertex at the IMJ (Fig. 1B). The starting angle between these two sides was based on the starting position of the bones in the observed feeding motion. The third side of the triangle was the resulting distance between the QMJ and the anterior tooth of the lower jaw, the effective mandible length, EM. In fishes without an IMJ, the EM is of fixed length, but in species with the novelty its length changes with rotation of the dentary relative to the articular. We then applied rotational movements of the dentary and articular to the original model configuration, recording changes in the cartesian coordinates of its vertices. This simulation resulted in the path of the lower jaw tooth following along a nearly straight line during the biting phase (Fig. S3), even with kinematics simplified to rotate at a constant rate, as noted above. To show that the lower jaw tooth in an IMJ system can also maintain consistent contact with a flat substrate during the biting phase, we retroactively constructed triangles to simulate the rotational angles and jaw positions needed to constrain lower jaw tooth movement along a flat substrate (i.e., to move along a straight line). We did the same to simulate movements of the lower jaw as it maintained contact with a concave substrate and a substrate with irregular contouring. R Code used for simulating movements can be found in archived data (see below).

RESULTS

Oral Jaw Morphology

The plesiomorphic state of the lower jaw within the family Distichodontidae is typical of most teleost fishes, with a single point of rotation at the QMJ and the articular firmly inserted into a triangle-shaped attachment in the posterior of the dentary, which causes the two bones to share a common orientation (Vari, 1979). While the articular in *D. sexfasciatus* also rotates about the QMJ, the general arrangement of mandibular bones in this species is highly modified and represents a strong departure from the general teleost form (Fig. 1A & B). The distal end of the articular is spatulate in shape, with its lateral face broadly overlapping the medial surface of a flattened and dorsally deflected dentary. At rest, the angle between the dentary and articular where they meet at the IMJ is approximately 65-degrees. Upper and lower jaws are linked via the *ligamentum primordiale*, which connects the lateral face of the dentary medially to the maxilla.

The muscles powering feeding movements in *D. sexfasciatus* are described briefly here and are illustrated in figure 1C and D. The adductor mandibulae complex contains four main subdivisions, with the first (A_1) originating ventrally on the quadrate just posterior to the QMJ and inserting anteriorly onto the medial surface of the maxilla on the upper jaw, near the bone's boundary with the premaxilla. The A_2 is further divided into a lateral segment (A_{2-l}) attaching medially and just below the dorsalmost point of the dentary and a medial segment (A_{2-m}) which gives way to a broad tendon that fuses with the tendon that extends anteriorly from the A_3 subdivision. The two aforementioned tendons converge on the posterior of the A_0 subdivision, which in turn attaches anteriorly across much of the distal (and medial) surface of the articular. Vari (1979) notes a ligamentous connection between the articular and dentary, and we augment this description, at least for *D. sexfasciatus*, to add that dorsal fibers of the A_0 also extend beyond the articular and attach at the dorsalmost point of the dentary. This connection appears to be the primary point of attachment for the overlapping plate-like portions of the dentary and articular, making it the likely center of rotation for the IMJ.

Kinematic Sequence of Jaw Components

Between the two feeding modes, suction-based motions of *D. sexfasciatus* displayed a more repeatable pattern, so we first discuss its general kinematics and then present biting motions relative to it. Prey capture motions consisted of three primary phases (Fig. 2). The first is characterized by expansion of the oral cavity as the gape gradually increases due to dorsal rotation of fused upper jaw bones (maxilla plus premaxilla) and extension of both the articular and dentary away from the head. The movements of lower jaw elements result in both ventral displacement of the teeth, but also in their anterior protrusion. This opening phase ends when the jaws achieve full gape and is followed by mouth closure or biting, where the teeth of the upper and lower jaws are rapidly brought together. Here, the upper jaw reverses direction and rotates ventrally. The articular also changes its rotation, now using flexion to move back toward the head, while extension of the dentary continues forward movement as it was in the opening phase. Finally, once the teeth on the upper and lower jaw have occluded (or nearly so, in some suction strikes), the jaws are retracted toward the head. During this phase there is continued rotation of the upper jaw ventrally (and now posteriorly), and the dentary and articular are once again moving in the same direction, back toward the head via flexion. The overall range of rotation for

lower jaw bones during suction-based feeding strikes was $27.40^\circ \pm 1.05^\circ$ s.e.m for the articular and $47.27^\circ \pm 1.23^\circ$ s.e.m for the dentary.

The kinematics of benthic biting are similar to that of suction feeding but differ in the extent of movements. Peak movements of both upper and lower jaw elements tend to be of smaller magnitude for biting motions compared to suction. For example, we observed minimal extension of the dentary during mouth opening (and sometimes even slight flexion), such that most of the movement of the lower jaw in this phase is achieved by forward extension of the articular. The range of rotation for during biting strikes was $24.06^\circ \pm 1.08^\circ$ s.e.m for the articular and $27.05^\circ \pm 1.48^\circ$ s.e.m for the dentary.

After an initial biting motion was completed, as described above, and with cucumber in clenched jaws, it was common to observe additional behaviors as the fish attempted to fully dislodge its food from the substrate. Particularly, a rocking motion of the jaws was used in which the articular and dentary repeatedly underwent rapid alternating cycles of extension and flexion until a piece of cucumber was removed (File S1). These motions included both a pulling action in a roughly perpendicular direction to substrate orientation that was driven by lower jaw movements, as well as lateral rotation of the oral jaws caused by side-to-side shaking of the entire head that presumably applied a shearing force on the substrate. We did not digitize these movements, both because they were highly variable in their application and shearing movements of the jaw system could not be captured with a lateral camera view.

Divergent Performance Outcomes: Lower Jaw Protrusion

Lower jaw protrusion was observed in all feeding strikes, although it was sometimes minimal during biting motions (Fig. 3), and within each feeding mode, individual fish did display significant differences ($P=0.0007$ for biting; $P=0.0001$ for suction). For this reason, we did not combine all individuals to compare jaw protrusion. In the two individuals that were compared statistically, suction feeding motions produced greater protrusion ($P=0.0005$ and 0.00025). While differences were observed between individuals, the effective mandible length (EM) across all fish displayed an average increase of $16.91\% \pm 2.38\%$ s.e.m. for biting motions and $51.99\% \pm 1.53\%$ s.e.m. for suction.

Single Performance Outcome: Modulation of Upper and Lower Jaw Movements

Jaw movement ratios – the relative displacement of lower jaw to upper jaw teeth during mouth closing – displayed largely overlapping ranges between biting and suction feeding (Fig. 4). However, 78% of suction-based motions had greater lower jaw versus upper jaw movement, compared to just 41% for biting strikes. No differences were observed between individuals ($P > 0.05$ for all pairwise comparisons), so fish were combined. Variance in jaw movement ratios for all fish was 2.5 times larger for biting motions ($s^2\text{-biting}=0.29$; $s^2\text{-suction}=0.12$; $P=0.0051$), suggesting a broader diversity of gape closing scenarios when teeth made contact with the prey. Plots tracking the movements of anterior teeth through space showed that during biting events there was substantial variation in the relative movement of jaws along the substrate (Fig. 5).

Versatility of Whole-Motion Kinematic Patterns

We found that within each feeding mode, individual fish had significantly different trajectory shapes ($P=0.0001$ for both suction and biting) and so we did not combine them for a single comparison between feeding modes. Instead, we did separate MANOVAs for the two fish that had several biting and suction strikes. In both, motion trajectories had significantly different shapes depending on feeding mode ($P=0.00095$ and 0.0011). These differences in trajectory shapes were evident in plots of scaled and aligned trajectories (Fig. 6) and suggested disparate kinematic patterns used to access benthic versus suspended prey. Trajectories for suction-based feeding events are characterized by comparatively smooth transitions in cranial shape between major phases of the feeding motion when compared to biting (note curvature of red versus blue average trajectories in Fig. 6). The distinction is particularly strong during the transition from the opening to closing phase, where shape change in biting motions takes a much more abrupt shift in directionality through shape space after peak gape, at the point when the teeth typically come in contact with the substrate.

Initial comparisons of kinematic variance did not show significant differences between individuals ($P > 0.05$ for all pairwise comparisons), so we combined fish for a single analysis. Here, we found that substrate biting motions are 2.04 times more kinematically variable than suction-based motions ($s^2\text{-biting}=0.13$; $s^2\text{-suction}=0.062$; $P=0.0001$). Taken together with the comparisons of average trajectory shapes above, these results are consistent with the idea that

jaw movements during biting are altered during interaction with the substrate and are more variable as a result.

Modeling Jaw-Substrate Interaction

Simulated lower jaw movements helped to illustrate how the IMJ facilitates the ability of *D. sexfasciatus* to maintain contact between its teeth and a benthic substrate through independent rotation of the dentary and articular (Fig. 7). In a manner similar to that observed in live fish, we recreate a kinematic pattern in which, 1) coordinated extension of both the dentary and articular away from the head both causes lower jaw protrusion and gape increase, 2) opposing movements of lower jaw bones, flexion of the articular but extension of the dentary, can produce a variety of patterns that comply to flat, curved and irregular surfaces, and finally 3) a return to coordinated movement, this time flexion back toward the head, results in the retraction of jaws and food. An important observation was that because of the inverted orientations of the dentary and articular (i.e., the lever arms of the model), the two bones must rotate in different directions to achieve the same direction of movement. For example, during coordinated forward extension in the opening phase (Fig. 7B), the articular rotates clockwise while the dentary rotates counterclockwise (red arrows in Fig. 7 C).

DISCUSSION

The intramandibular joint is a specialization for benthic feeding, and in *Distichodus sexfasciatus* provides versatility for context-dependent modulation of prey capture kinematics. In contrast to most other teleost fishes, the feeding mechanism features dissociated articular and dentary bones that can move quasi-independently of each other. This has resulted in a lower jaw capable of complex movement and an ability to modulate those movements while feeding on different prey and during varying scenarios of jaw-substrate interaction. A central finding of this study is that patterns of rotation between the lower jaw bones change during feeding and account for the distinct movements produced during each of three motion phases. The articular and dentary move in the same direction during mouth opening, in different directions during closing (peak gape to occlusion), and again in the same direction during retraction of the jaws back toward the head (Fig. 2). This ability is likely enabled by a muscle arrangement where the A_{∞} subdivision of

the adductor complex attaches to both lower jaw bones, but the A_{2-1} attaches solely to the dentary, allowing independent control of this bone (Fig. 1). Additionally, the antagonistic movements of lower jaw bones during the closing phase allow the teeth to follow along a flat plane with the substrate (Figs. 5 & 7). This interaction with the substrate is simply not possible for fishes lacking an IMJ without coordinated movements of the body, as their mandible has a single point of rotation and movements of the teeth are consequently constrained along an arc-shaped path.

The IMJ in *D. sexfasciatus* is similar to other examples of the novelty in teleost fishes in that flexibility between the articular and dentary contributes to gape widening while approaching the substrate (Purcell and Bellwood 1993; Gibb et al. 2008; Ferry-Graham and Konow 2010; Ferry et al. 2012), but there is also evidence that it plays a role in gape constriction as observed in some pomacanthids (Konow and Bellwood 2005; Konow et al. 2008). This is most readily observed in suction feeding strikes, where rotation of the dentary contributes to jaw closing while in a protruded lower jaw state (Fig. 2). Mean angles of rotation at the intramandibular joint in *Distichodus* were approximately 47° for suction feeding and 27° for biting, which is of similar magnitude to values reported for IMJ-bearing butterflyfishes (Chaetodontidae), Angelfishes (Pomacanthidae), and a host of other reef-associated fishes (Konow and Bellwood 2005; Konow et al. 2008). Still, these all fall well short of the spectacular $90^\circ+$ IMJ rotation observed for the freshwater molly, *Poecilia sphenops* (Gibb et al. 2008).

An interesting distinction from some other IMJ-bearing species is that *Distichodus* has a fused upper jaw (maxilla and premaxilla) that rotates as a single structure. This contrasts the independently mobile upper jaw bones in other taxa that allow for upper jaw protrusion, like chaetodontids, but may be more similar in function to the upper jaws of most acanthurids. Another difference was observed behaviorally in the form of rapid and repeated rocking movements of lower jaw bones that were used to dislodge attached prey (File S1). These movements, which have not been previously documented in species with an IMJ, were highly variable and consisted of one to over ten cycles of pulling in the anterior-to-posterior direction. They were characterized by extensive rotation of both the articular and dentary and were sometimes supplemented by side-to-side movements of the head. One possibility is that the combination of pulling and shearing movements, and the ability to use just one or both methods, confers greater control in the manner and extent that force is applied while removing attached

prey. This behavior, and other complex movements noted above, likely improve access to and removal of attached prey, illustrating that the IMJ provides a number of specialized functions for benthic feeding fishes.

Role of IMJ in Jaw Versatility

Complex movements of the lower jaw in *D. sexfasciatus* were observed during both benthic biting and suction feeding (Figs. 2 & 3). We provide evidence in support of our initial prediction that the IMJ plays an integral role in the ability of this jaw system to modulate feeding kinematics in a versatile manner. First, we showed that divergent performance outcomes were achieved for suction and biting strikes. Whole-motion kinematic patterns differed by feeding mode (Fig. 6) and protrusion was greater for suction feeding compared to biting (Fig. 3). We find this difference in jaw protrusion to be particularly compelling, as it comports with classic expectations of oral jaw function (Westneat, 1994). Higher levels of protrusion during suction act as a form of lower jaw ram, moving the jaw forward toward more elusive mid-water prey. In contrast, lower protrusion during substrate biting is consistent with the ability to shorten the jaw's out-lever length for tuning bite force (Ferry-Graham and Konow, 2010).

The second form of versatility displayed by *D. sexfasciatus* results in the ability to modulate movement while maintaining a single performance outcome. Variance in whole-motion kinematic pattern is two times greater for biting, reflecting the different ways in which the lower jaw adjusts and complies to the substrate. Suction feeding kinematics were useful as a source of comparison to benthic biting because the motions were far more repeatable and illustrated the unimpeded movements of the feeding apparatus. One source of increased kinematic variance during benthic biting were differences in relative movements of upper versus lower jaws (Fig. 4) – the teeth from one jaw would occasionally engage with the substrate first, become lodged, and flexibility at the IMJ would then allow the other jaw to move dorsally (lower jaw) or ventrally (upper jaw) along the surface of the substrate to meet it (Fig. 5). One currently unresolved question is whether increased modulation during biting is due to active neuromotor control of the jaw system in response to the various scenarios of jaw-substrate interaction shown in figure 5, a passive response to it, or a combination of the two. Certainly, active control exists during gape closure, as evidenced by independently rotating lower jaw

bones during suction-based strikes in the absence of external influence from the substrate (Fig. 2).

The capacity for more complex motions in lower jaws containing an IMJ ensures a greater number of possible kinematic outcomes compared to mechanically simpler mandibles. The link between morphological complexity and functional versatility is well known (Vermeij 1973; Wainwright 2007; Price et al. 2010), and it follows that a specialization for benthic biting favors greater kinematic variation for that feeding mode. In fact, the IMJ represents an intriguing parallel to the dissociation of upper jaw bones (maxilla and premaxilla) and the diversity of suction-based kinematics, what Karel Liem (1980) called the feeding repertoire (also see Van Wassenbergh and De Rechter 2011). Versatility and an ability to modulate feeding kinematics can be helpful for feeding from different substrate topologies (Fig. 7), but also for accessing temporally variable benthic food resources that require different methods of biting for prey removal, like filamentous algae from a rocky surface versus parts of leaves from aquatic vegetation (Inyang and Nwani 2004; Mbadu Zebe et al. 2010).

The IMJ and Functional Innovation

Phenotypic novelties occasionally result in functional innovation, where organisms possessing the novelty have enhanced ability to access resources compared to those lacking it (Wainwright and Price 2016). Innovations can fundamentally alter the adaptive landscape for the structure in question and may lead to increased morphological (Price et al. 2010) or lineage (Dumont et al. 2011) diversification, but their impacts are varied and often mixed (Dornburg et al. 2011; Konow et al. 2017; Burrell and Wainwright 2019). An argument can certainly be made that intramandibular mobility by way of an IMJ constitutes a functional innovation. In *D. sexfasciatus* alone, we found that the joint enables a suite of functions not possible with the typical fused teleost mandible. These include lower jaw protrusion as a form of ram, modulation of mouth closing kinematics to maintain contact with substrate, and pulling movements (independent from body input, but sometimes supplemented by it) to remove attached prey.

Clearly, the IMJ allows fishes to feed in ways that others cannot. However, something that remains unclear is the role, if any, that the joint has played in the morphological and lineage diversification of distichodontid fishes. While many species in the family have some degree of intramandibular flexibility, only those within *Distichodus* and *Nannocharax*, a genus of mostly

benthic invertivores (Lavoué et al. 2017), have highly mobile IMJs (Vari 1979). Moreover, these two genera (out of 16 total) account for over 60 percent of the species diversity across Distichodontidae (Froese and Pauly 2021), and it is conceivable that the highly mobile IMJ that the two share is associated with elevated lineage diversification. Future work is needed to address this hypothesis, including improved phylogenetic resolution on inter-generic relationships (Arroyave et al. 2013; Lavoué et al. 2017).

Ecological significance of the IMJ

The IMJ has independently evolved several times across teleost fishes (Konow et al. 2008; Gibb et al. 2015; Wainwright and Longo 2017), and in nearly all cases it is associated with species that feed by removing attached prey from benthic surfaces. The novelty, therefore, appears to be a repeated evolutionary solution to a common set of functional challenges. Compared to the more common suction-based feeding mode in teleosts, removal of attached prey requires greater jaw closing forces and an ability to respond to variation in the substrate's structure (Ferry-Graham and Konow 2010; Mackey et al. 2014). Many examples of IMJs occur in coral reef systems, providing species with greater access to prey on the abundant hard benthic substrates found in these habitats (Konow et al. 2008). There is less information about the presence of IMJs in freshwater fishes, but examples can be found in poeciliids (Gibb et al. 2008) and the monotypic Helostomatidae (Ferry et al. 2012), species that at least occasionally graze on benthic algae. Despite the fact that a majority of herbivorous fishes occur in freshwater habitats (Tolentino-Pablico et al. 2007), the topic is understudied and there are likely other examples of independently acquired intramandibular mobility in these systems (Gibb et al. 2015)

Available dietary information suggests that *Distichodus* consists of primarily herbivorous species (Arawomo 1982; Inyang and Nwani 2004; Berté et al 2008; Mbadu Zebe et al. 2010; Dietoa et al. 2014). Although there are no radical departures in the genus from the jaw system shown here for *D. sexfasciatus*, there is likely functionally relevant morphological variation across species. These are mostly associated with terminal versus subterminal mouths and relative snout length (Vari 1979; Arroyave et al. 2020). Previous work in closely related species of IMJ-bearing surgeonfishes (Acanthuridae) shows that small to moderate differences in jaw morphology can result in species that access different benthic prey from the same substrate type (Purcell & Bellwood 1993). Additionally, marine angelfishes (Pomacanthidae) with IMJs display

low functional variation, but high trophic diversity (Konow and Bellwood 2011). It is possible that closer examination of the prey consumed and specific nutrients accessed in other *Distichodus* species will reveal greater diversity in their feeding ecology.

Conclusion

In the herbivorous *D. sexfasciatus*, the intramandibular joint results in a lower jaw system capable of complex movements, enhancing benthic biting performance and the ability to modulate feeding kinematics for different prey and during interactions with the substrate. We show empirically that the independent movement of lower jaw bones enabled by this novelty allows teeth to maintain contact with flat benthic surfaces, and a modeling exercise points to the possibility of the jaw system conforming to different substrate topologies. While this study provides new insights about the function of the IMJ in an understudied system, a number of questions remain. For example, dentition is highly variable across biting fishes and plays a vital role in benthic feeding (e.g., Streit et al. 2015), but it is unclear how or whether variation in tooth morphology can mediate disparities in feeding performance between species with and without an IMJ. Additionally, we did not consider how the function of the IMJ changes through ontogeny, although we know that flexibility of the joint can change with size (Dial et al. 2017). Lastly, we believe a case can be made for the IMJ as an example of morphological, and possibly functional, convergence in fishes, but broad comparative study is needed. Much like our study species, we have just scratched the surface.

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Competing interests

The authors declare no competing or financial interests.

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Data Availability

Data and R code used in this study are available in the Dryad data repository:
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Figures

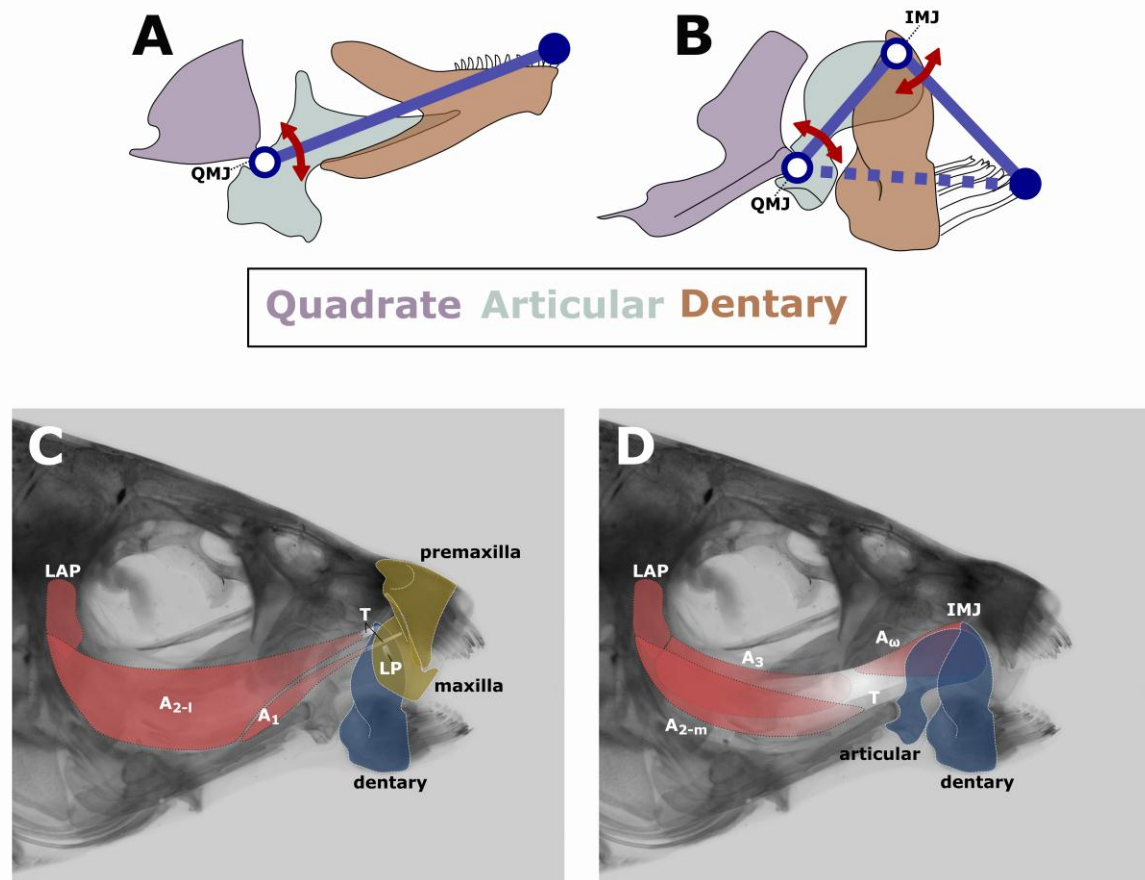


Figure 1. Morphological features of the oral jaws involved in prey capture. Diagrams show differences in jaw function between (A) a mandible of a typical teleost (*Paratilapia polleni*) with a single point of rotation at the quadratomandibular joint (QMJ), and in (B) *Distichodus sexfasciatus*, which possesses a secondary point of rotation at the intramandibular joint (IMJ). Identities of lower jaw bones are color coded and listed below. The distance from the QMJ and the distal tooth of the lower jaw, shown as a dashed line, represents the effective mandible length, EM. (C & D) Muscles powering movements of oral jaws and their attachments are drawn on a photograph of a cleared and stained specimen. Abbreviations after Vari (1979): A₁= first subdivision of the *adductor mandibulae* muscle complex (*a.m.*); A₂₋₁, lateral segment of the second subdivision of the *a.m.*; A₂₋₁= medial segment of the second subdivision of the *a.m.*; A₃= third subdivision of the *a.m.*; A₀= omega subdivision of the *a.m.*; LAP= *levator arcus palatini*; LP= *ligamentum primordiale*; T= tendon.

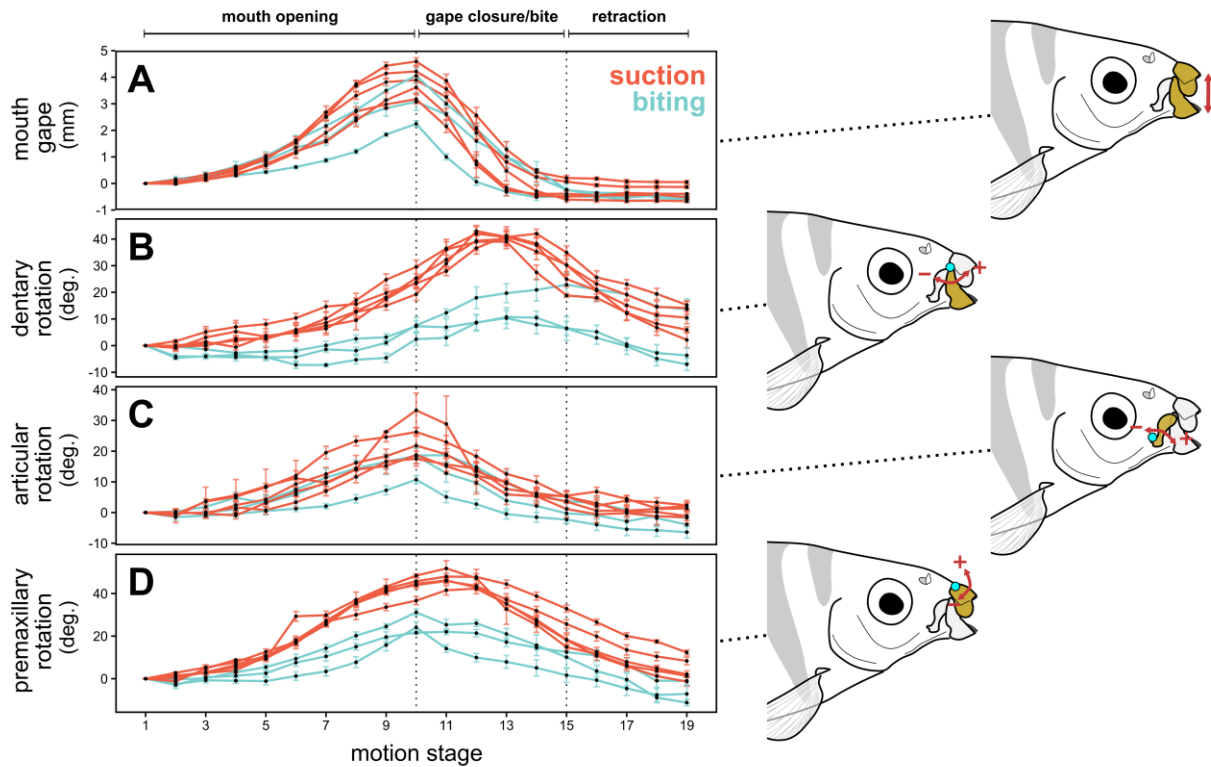


Figure 2. Sequences of movement for key morphological features across 19 motion stages in biting and suction-based strikes ($n=64$ motions; 22 biting, 42 suction). Traits include, (A) mouth gape, (B) rotation of the dentary about the IMJ, (C) rotation of the articular about the QMJ, and (D) rotation of the premaxilla about the supraethmoid. In each panel, mean trait values (\pm s.e.m.) of individual fish are shown by a single line ($n_{\text{suction}}=5$ individuals; $n_{\text{biting}}=3$ individuals). Drawings to the right of traits highlight morphological features involved in measurements, with + and – symbols indicating rotational directions resulting in larger and smaller plot values, respectively. Dashed vertical lines mark peak gape (left) and occlusion of teeth (right), separating three main phases of feeding motions. Suction and biting display similar patterns, but values for biting motions are often smaller, indicating less movement.

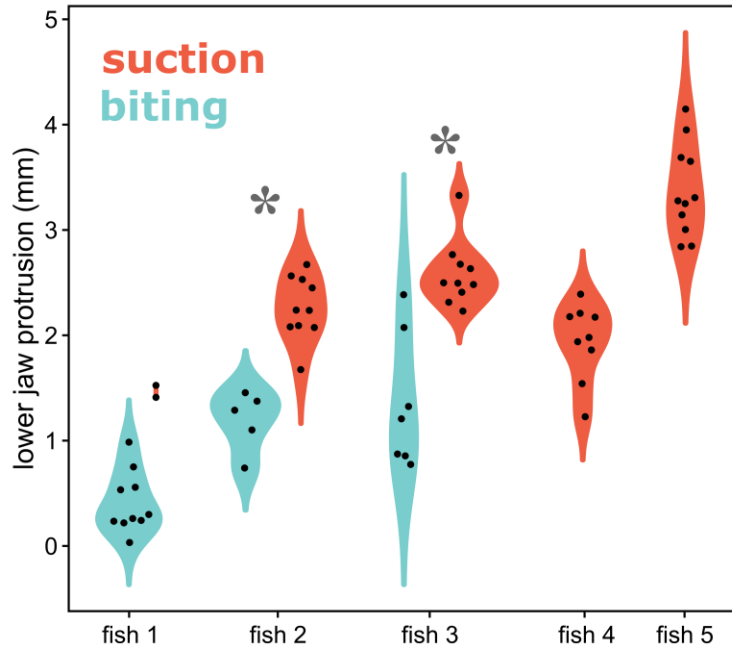


Figure 3. Protrusion of the lower jaw plotted by fish identity for suction and biting strikes (when present). Separate ANOVAs comparing mean values in fish 2 and 3, denoted with asterisks, indicate greater protrusion during suction feeding ($P < 0.001$ for both tests).

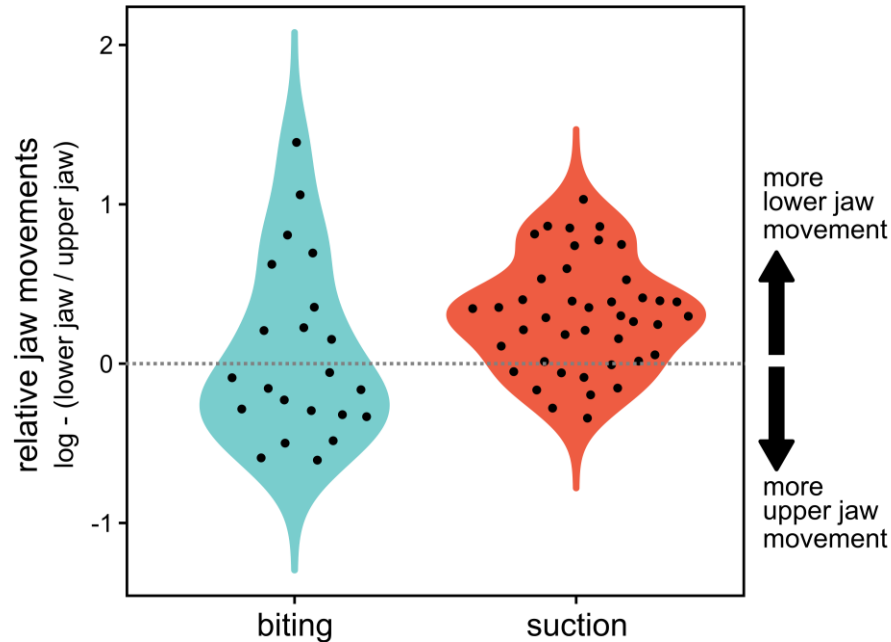


Figure 4. Comparisons of lower versus upper jaw movements during the closing phase of feeding motions, from peak gape to occlusion of the teeth ($n=64$ motions; 22 biting, 42 suction). Values shown are the natural logarithm of the ratio of lower jaw movement to upper jaw movement. The dotted line shows the point at which upper and lower jaws move the same distance, with larger values indicating greater lower jaw movement and smaller values greater upper jaw movement. While the ranges are broadly overlapping for the two feeding modes, biting motions ($n_{\text{biting}}=3$ individuals) have over two times greater variance than suction ($n_{\text{suction}}=5$ individuals), reflecting modulation of kinematics due to jaw-substrate interaction (Variance test; $P= 0.0051$).

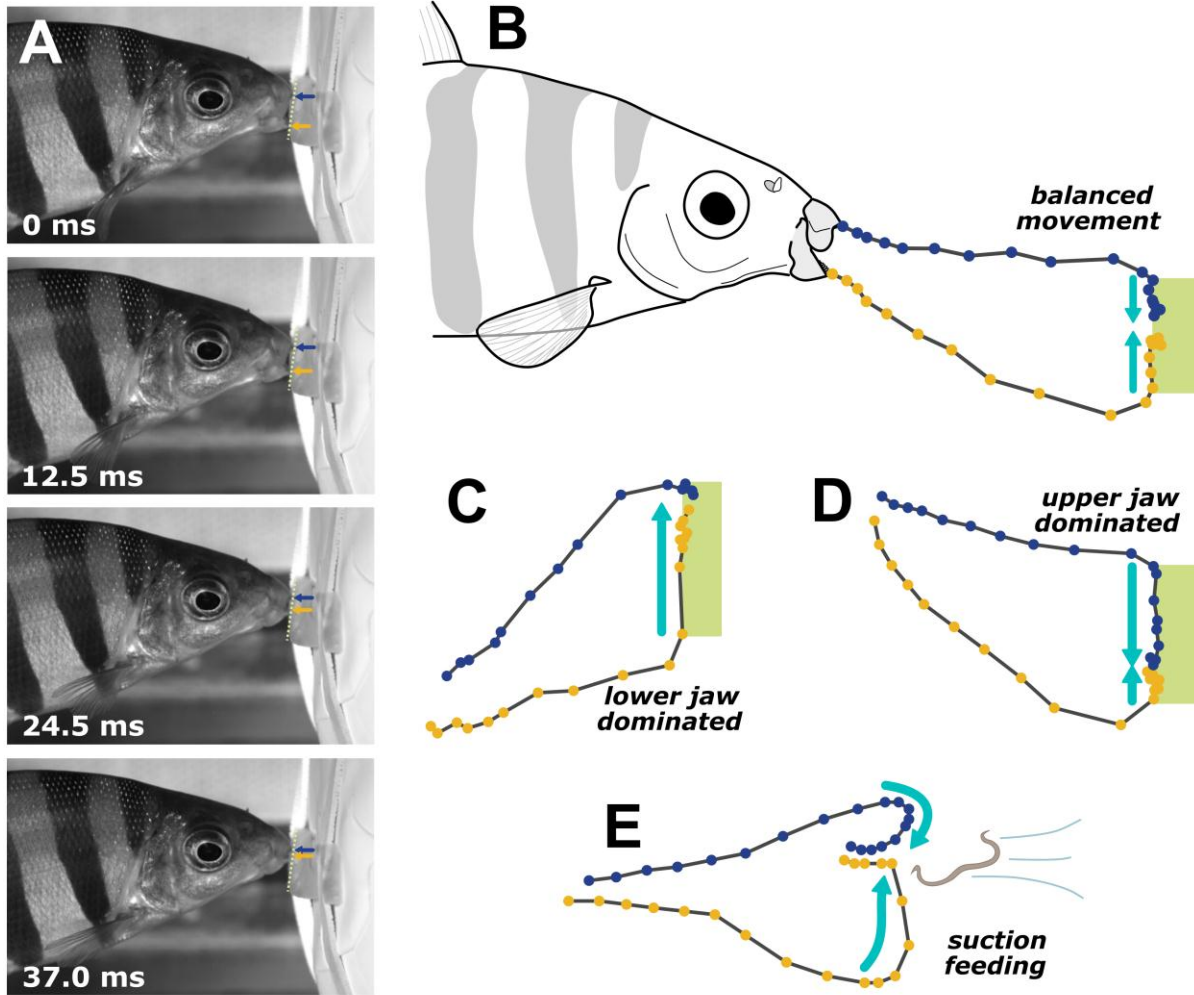


Figure 5. Scenarios of jaw-substrate interaction. (A) A series of video frames taken during the biting phase of a feeding motion, showing first contact with the substrate on top and occlusion of the teeth on the bottom. Here, the upper jaw teeth (blue arrow) are lodged in the substrate, while the lower jaw teeth (yellow arrow) scrape upward along a flat plane to maintain contact with the food. Movements of anterior tooth landmarks are tracked for representative feeding events, illustrating modulation of jaws relative to the substrate. Points along the teeth tracks indicate their positions relative to the food, and include forward movement associated with swimming towards the prey and biting movements of the oral jaws during the mouth closing phase (light blue arrows). Variants include (B) roughly equivalent upper and lower jaw movements, (C) lower jaw dominated biting, (D) upper jaw dominated biting, and (E) a suction feeding event with no intentional contact with the prey. Note that in each of the biting examples shown, the jaw maintains contact with the substrate by moving along a flat plane.

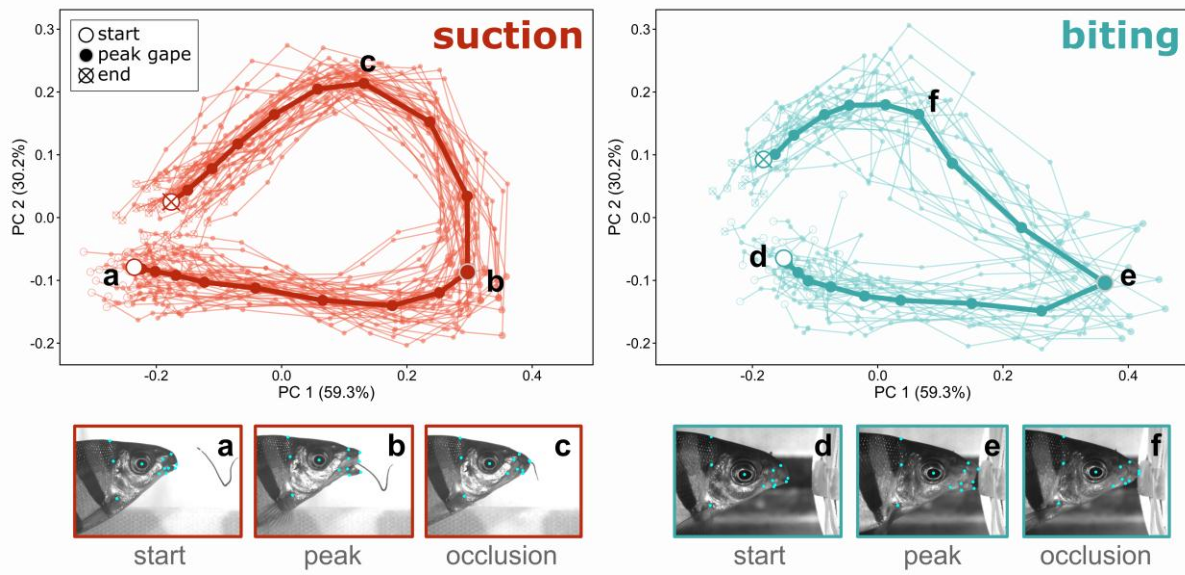


Figure 6. Principal component axes 1 and 2 for Procrustes-aligned shape trajectories, showing 64 feeding motions ($n_{\text{suction}}=42$; $n_{\text{biting}}=22$) in *D. sexfasciatus*. Biting and suction are shown in separate panels for visualization but were part of a common alignment and PCA. Each line represents a single feeding strike and points along them are consecutive cranial shapes at different stages of the motion. Note that in this plot, the subject of alignment was not individual cranial shapes, as is traditionally done in geometric morphometrics, but the shapes of the trajectories that they produce. Mean trajectories for each feeding mode are shown as bold lines. Suction-based trajectory shapes appear to follow a more repeatable pattern (i.e., are less variable) than those for biting. Representative video frames with cranial landmarks are shown for the start of the motion (a, d), peak gape (b, e), and occlusion of the teeth (c, f). While only two dimensions are displayed here, all statistical comparisons of trajectories in this study were done in the full dimensionality of the shape data. Separate MANOVAs in two individuals, comparing mean trajectory shapes, suggest divergent kinematic patterns for biting versus suction motions ($P < 0.01$ for both tests).

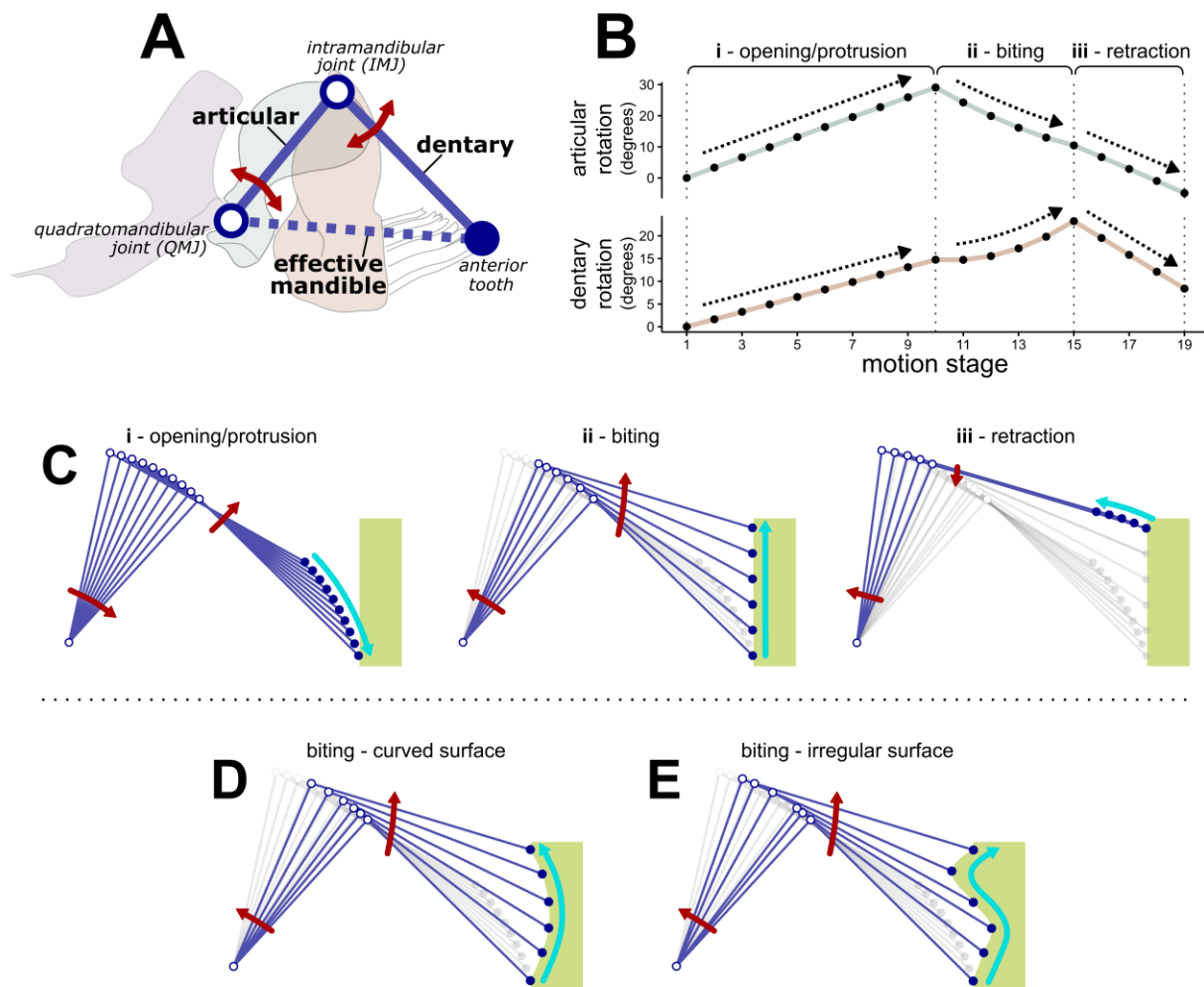


Figure 7. Simulated movements of the lower jaw in *D. sexfasciatus*. (A) The jaw system is modeled as a triangle with two sides representing lever arms of fixed length for the articular and dentary. The third side is the effective mandible length (EM), from the base of the jaw (QMJ) to the anterior lower jaw tooth, which varies in length with rotation the dentary about the IMJ. (B) Rotation was applied to the lever arms of the model, based on ranges observed in a live fish. Note that both bones display forward extension (increasing values) during the opening phase, move in opposing directions during the biting phase, and then both show flexion (decreasing values) during jaw retraction. (C) Simulated movements of the lever arms are shown with red arrows indicating the directions of rotation and blue lines showing the path taken by the lower jaw tooth. Note that due to the inversion of lever (bone) orientations opposing directions of

rotation result in similar directions of movement relative to the prey (e.g., forward extension is achieved through clockwise rotation of the articular but counterclockwise rotation of the dentary). Teeth were made to maintain contact with a flat, vertical substrate during the biting phase, but are also shown for a **(D)** curved and **(E)** irregular surface.



Fig. S1. Photo showing setup for benthic biting in this study. A vertically oriented slice of cucumber is strapped to a ceramic block with rubber bands.

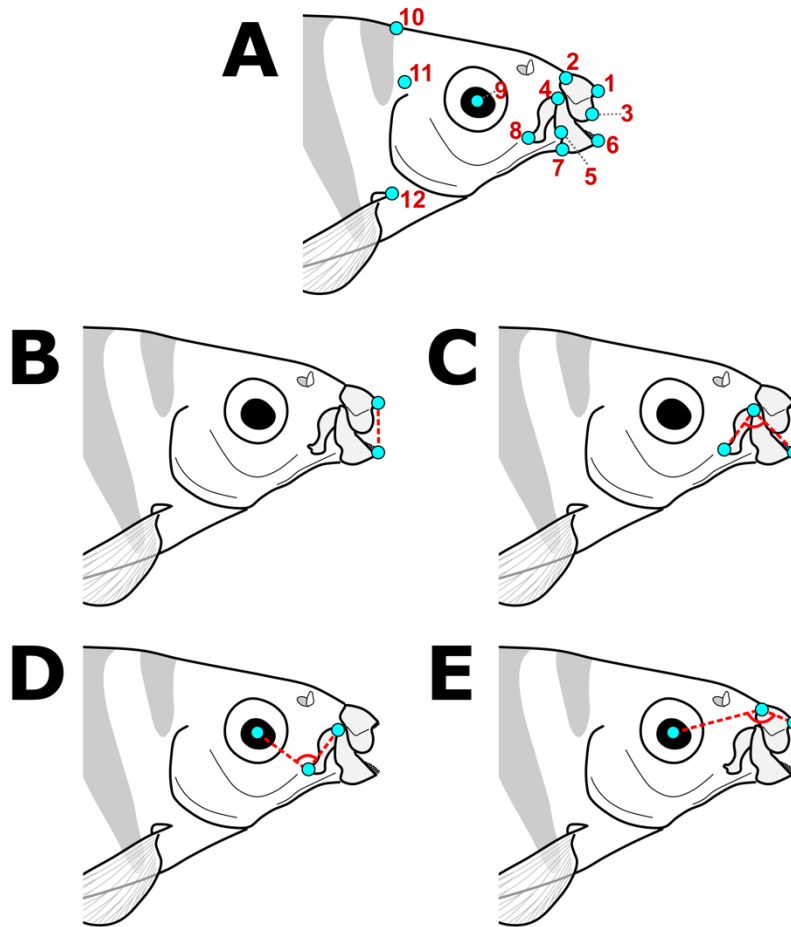


Fig. S2. (A) Cranial landmarks used to capture feeding kinematics in *Distichodus sexfasciatus* and subsets used to measure (B) gape, (C) rotation of the dentary about the IMJ, (D) rotation of the articular about the QMJ, and (E) rotation of the upper jaw. Landmarks are as follows: 1) anterior tooth of premaxilla, 2) supraethmoid-premaxilla joint, 3) anteroventral corner of maxilla, 4) intramandibular joint, 5) posteroventral sulcus of dentary, 6) anterior tooth of dentary, 7) posteroventral corner of dentary, 8) quadratomandibular joint, 9) center of eye, 10) dorsal outline directly above pectoral fin landmark, 11) supracleithrum-posttemporal (head) joint, 12) dorsal base of pectoral fin.

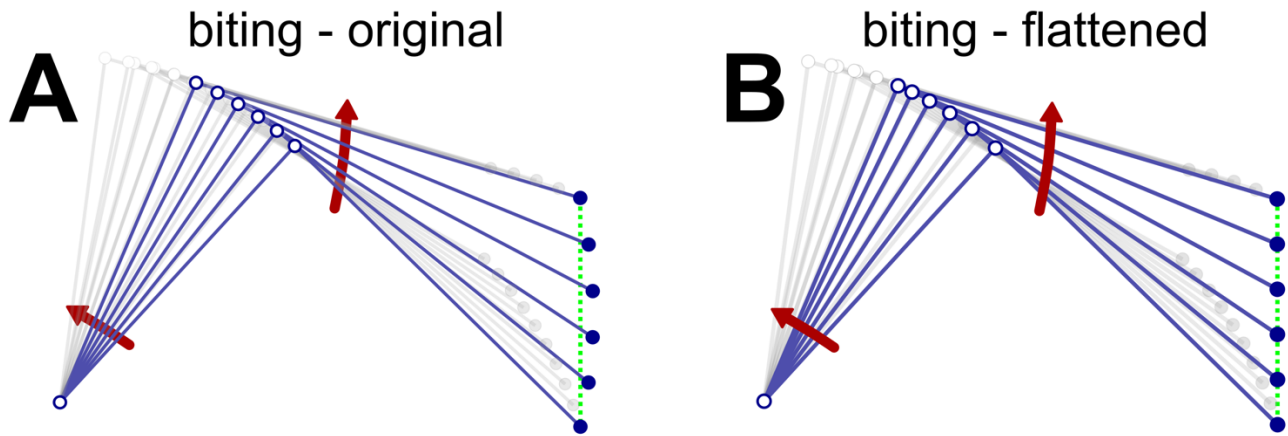
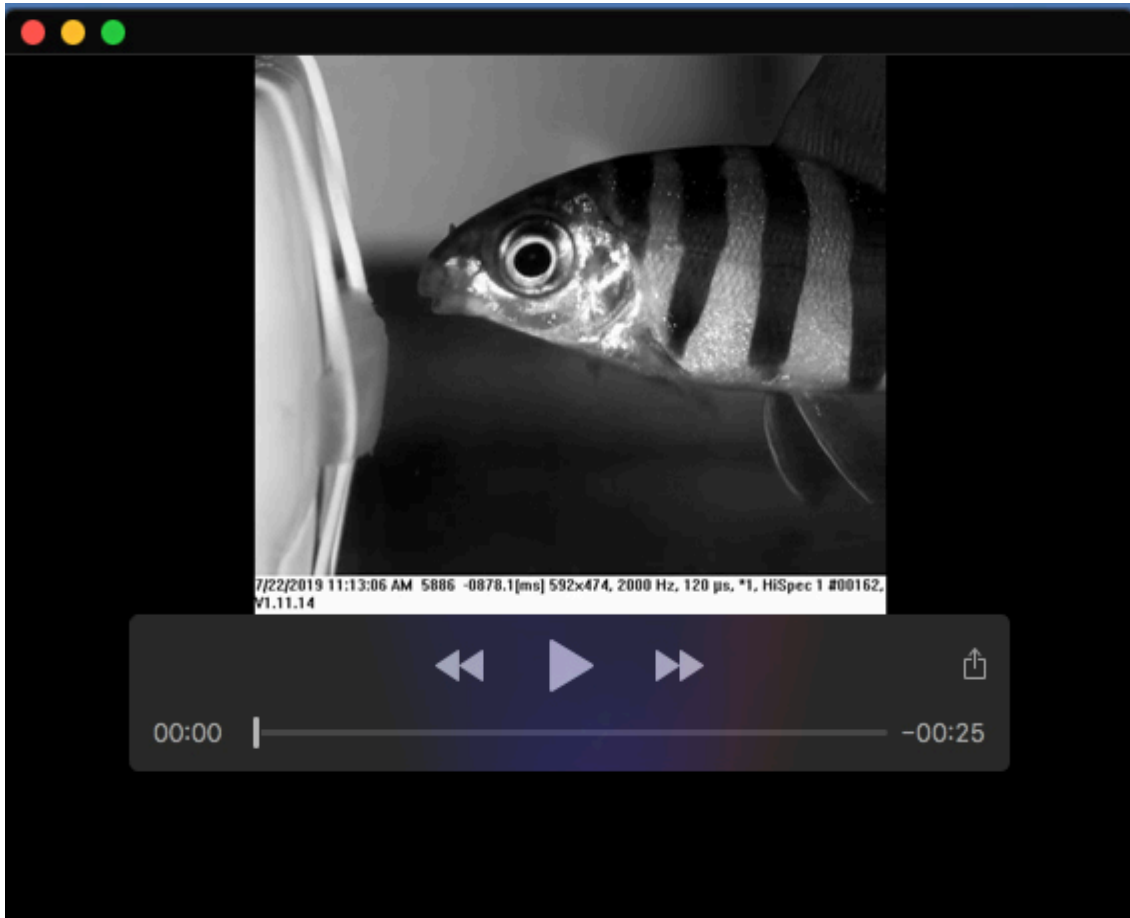


Fig. S3. Simulated closing motions of the jaw system in *D. sexfasciatus*. (A) Originally, rotational input of jaw levers is simplified to maintain a contact rate of movement from stage to stage and the resulting tooth path was nearly flat (green dotted line). (B) We calculated the rotation and position of jaw levers necessary for teeth to move along a perfectly flat path during biting.



Movie 1. High-speed video showing repeated pulling movements of the jaws to remove attached benthic prey.