

# The Intramandibular Joint in *Girella*: A Mechanism for Increased Force Production?

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**ABSTRACT** Intramandibular joints (IMJ) are novel articulations between bony elements of the lower jaw that have evolved independently in multiple fish lineages and are typically associated with biting herbivory. This novel joint is hypothesized to function by augmenting oral jaw expansion during mouth opening, which would increase contact between the tooth-bearing area of the jaws and algal substratum during feeding, resulting in more effective food removal from the substrate. Currently, it is not understood if increased flexibility in a double-jointed mandible also results in increased force generation during herbivorous biting and/or scraping. Therefore, we selected the herbivore *Girella laevis* for a mechanical study of the IMJ lower jaw lever system. For comparative purposes, we selected *Graus nigra*, a non-IMJ-bearing species, from a putative sister genus. Shortening of the lower jaw, during flexion at the IMJ, resulted in a more strongly force-amplifying closing lever system in the lower jaw, even in the absence of notable changes to the sizes of the muscles that power the lever system. To explain how the IMJ itself functions, we use a four-bar linkage that models the transmission of force and velocity to and through the lower jaw via the IMJ. When combined, the functionally interrelated lever and linkage models predict velocity to be amplified during jaw opening, whereas jaw closing is highly force modified by the presence of the IMJ. Moreover, the function of the IMJ late during jaw closure provides enough velocity to detach sturdy and resilient prey. Thus, this novel jaw system can alternate between amplifying the force or the velocity exerted onto the substrate where food items are attached. This unique mechanical configuration supports the argument that IMJs are functional innovations that have evolved to meet novel mechanical challenges and constraints placed on the feeding apparatus by attached and sturdy food sources. *J. Morphol.* 000:000–000, 2009. © 2009 Wiley-Liss, Inc.

**KEY WORDS:** levers; four-bar linkage; herbivory; biting; functional innovation

## INTRODUCTION

The biting mode of prey capture in aquatic feeding vertebrates is a remarkable phenomenon from both an ecological and an evolutionary perspective. Morphologically, biting is thought to be correlated with an increase in the complexity of the skeletal elements used for prey capture (Wainwright and

Bellwood, 2002). This is likely due to the forces required for obtaining food items many of which are either tough or firmly attached to the substrate (Alfaro et al., 2001). In several reef fish lineages, aspects of the feeding apparatus have been radically altered for force production, either via hypertrophied or via structurally altered musculature (Friel and Wainwright, 1997), modified muscle attachments (Vial and Ojeda, 1990; Konow and Bellwood, 2005), or increased suturing and/or reinforcement of bony elements and dentition (Tedman, 1980; Streelman et al., 2002; Bellwood et al., 2003). Meanwhile, some biting lineages seem to rely on entirely different solutions for prey acquisition, likely to meet the novel demands of their mechanically and topographically challenging feeding substrata.

Among the latter type of modifications is a novel joint within the mandible or lower jaw, as seen in some acanthurids (Purcell and Bellwood, 1993), blennids (Konow and Bellwood, 2005), poeciliids (Gibb et al., 2008), scarids (Tedman, 1980; Streelman et al., 2002), and girellids (Vial and Ojeda, 1990, 1992). This intramandibular joint (IMJ) was independently derived in each of these lineages (Konow et al., 2008), and yet, it is consistently associated with a predominantly dislodging mode of feeding on herbivorous diet items. Herbivory is associated with a broad suite of behaviors loosely categorized as biting. These include scraping, excavating or gouging, and shearing. Such methods of food acquisition are required when the target items are physically durable or difficult to dislodge from the substrate, as can be the case with many

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marine algae (Steneck and Dethier, 1994). Algae, a polyphyletic grouping that includes the macroscopic Phaeophyceae, Rhodophyta, and Chlorophyta, each possess many traits that directly or indirectly provide some impediments to marine herbivores. These include cellulose and other fibrous structures (Martone, 2007), lignin (in red algae; Martone et al., 2009), and calcification (Steneck and Martone, 2007). In the case of the large and resilient brown algae, for example, a fish might only be able to extract small pieces from whole fronds via biting or cutting. However, even very small food items, such as algal or diatom films, can require elaborate methods to scrape and detach them from the hard substrate (Purcell and Bellwood, 1993).

In most cases, IMJs are thought to permit an increased dorsoventral expansion of the oral jaw gape, yielding a larger tooth-bearing surface that provides increased contact with algal-covered substrates (Kanda and Yamaoka, 1995). This mechanism may thereby potentially yield a quantitatively more effective scraping bite for removing food (Bellwood et al., 2003). For one freshwater omnivore, it has also been proposed that the IMJ may allow the teeth to more effectively “comb” through periphyton, sieving out small invertebrates, using similar jaw movements as described for the marine species above (Gibb et al., 2008).

The forces produced by the jaws during feeding have been effectively modeled using engineering models of lever and linkage function (Westneat, 2004). While being a mechanical construct, biomechanical levers and linkages still reflect the underlying morphology of the jaw (Westneat, 1990). One strength of this approach is that such biomechanical representations have clear functional interpretations (Wainwright and Richard, 1995) and therefore can accurately reflect the ecological consequence of changes to the morphology of the jaw bones and muscles. Species should separate based on the force and velocity transmitting capabilities of their jaws, which is reflected in the measurements of transmission coefficients from the lever and linkage systems. Biomechanical systems are generally thought incapable of simultaneously being speed and force amplifying, and indeed, most species tend to occupy one end or the other of a continuum, being either capable of slow, forceful movements, or rapid but weak movements.

We selected *Girella laevisfrons* for mechanical study of how the IMJ affects the jaw lever system. This species uses both algal and invertebrate material in the diet (Aldana et al., 2002), like most *Girella* species (Kanda and Yamaoka, 1995; Clements and Choat, 1997). *Girella laevisfrons* has been described as consuming the durable brown algae *Macrocystis integrifolia*, as well as more ephemeral brown and foliose red algal species (Pérez-Matus et al., 2007). For comparative purposes, we choose *Graus nigra*, from the putative sister genus to

*Girella* (Johnson and Fritzsche, 1989). Both species are members of the Kyphosidae (Yagishita et al., 2002; Nelson, 2006). *Graus nigra* has been described as having an herbivorous diet at certain life history stages (Aldana et al., 2002) and is thought to have a different suite of mechanisms for creating a forceful bite, most notably hypertrophied jaw muscles. Importantly, this species lacks the intramandibular jaw joint (Vial and Ojeda, 1992).

Our specific aims in this study were to measure and contrast the jaw lever ratios in *Girella laevisfrons* and *Graus nigra* to test the hypothesis that there is a quantifiable force advantage conferred by the IMJ. We also investigated the lower jaw depressor and adductor musculature to determine whether other morphological changes associated with force production were observed either in addition to or in lieu of an advantage conferred by the IMJ. Finally, we propose a four-bar linkage model to explain how forces are transferred to and through the IMJ during biting.

## METHODS

Specimens of *Girella laevisfrons* and *Graus nigra* were obtained using SCUBA and pole spear from Punta Teatinos (29°49'S, 71°22'W) and Caleta de Hornos (29°37'S, 71°19'W) in Northern Chile. Ten individuals of each species were obtained, which ranged in size from 21.5 to 39.5 cm total length (TL; average 32.5 cm) for *Girella*, and from 35.0 to 61.0 cm TL for *Graus* (average 49.8 cm). The chosen specimens intentionally spanned a range of sizes because both species are known to use varying degrees of algal material throughout ontogeny, with both species potentially increasing their reliance on algal material with age, and *Graus* secondarily switching back to carnivory at large body sizes (Johnson and Fritzsche, 1989; Aldana et al., 2002). Such diet shifts may be associated with changes in morphology that should not be ignored. *Graus* specimens were on average larger than *Girella* as is reflective of their natural distributions; mature *Graus* achieve a much larger body size. Specimens were fixed in 10% formalin and stored in 70% ethanol until dissected.

The following morphometric variables were quantified for each dissected individual total length (TL, cm); head length (HL, cm); mass of the adductor mandibulae 2 muscle (AM2, g); mass of the sternohyoideus muscle (SH, g); length of the jaw out-lever (cm); length of the opening in-lever (cm); and length of the closing in-lever (cm). Muscle masses were obtained by dissecting the muscles completely from the head, blotting the muscles dry, and weighing them to the nearest 0.01 g. Lengths of the lower jaw in- and out-lever arms were measured using a dial caliper to the nearest 0.1 mm, and following the protocol outlined in previous studies (Wainwright and Richard, 1995; Wainwright and Shaw, 1999). The exception is the determination of the jaw closing out-lever length in *Girella*. The lower jaw in most fishes is composed of the dentary and the angular-articular. These two components are typically rigidly fused so that the out-lever length does not change during mouth opening or closing, as is the case in *Graus*. However, in the genus *Girella* the association between these two bony elements involves a mobile joint (the IMJ), permitting the anterior dentary portion of the mandible to flex ventrally during jaw opening due to the action of the geniohyoideus (GH) muscle (Vial and Ojeda, 1990, 1992). Manipulations of both *Girella laevisfrons* and cleared and stained *Girella nigricans* (from California) reveal that mechanically, this additional lower jaw flexion (Fig. 1C) causes a reduction of the length of the out-lever by about 20%. Video of *Girella nigricans* feeding (Supporting Information video) confirms that flexion at this articulation attains about 20°.

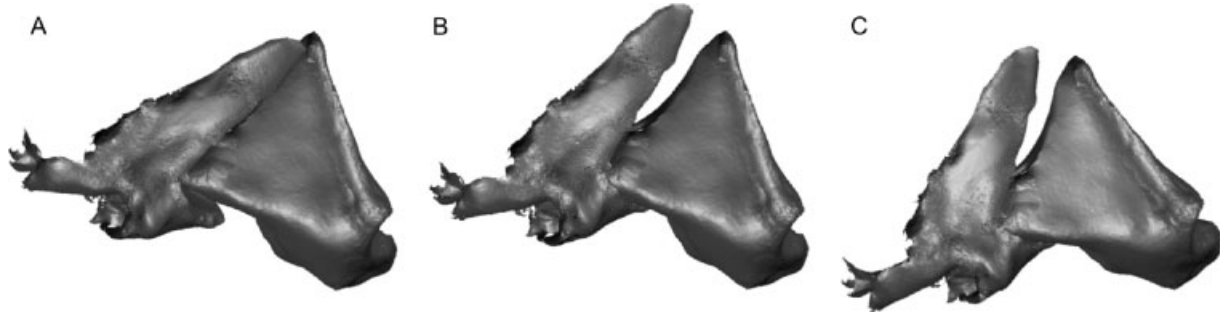


Fig. 1. Renderings of the left lower jaw of *Girella* (see Methods). In each picture, dentary tooth surface (poorly rendered) faces left and lower jaw articulation (LJA) faces right. The intramandibular joint is where the articular invades the dentary bone. **A**: resting position; **B**: Intramandibular joint rotated; **C**: Intramandibular joint rotated and lower jaw depressed.

Each morphometric variable was analyzed for ontogenetic shape changes by regressing against TL for each species. Specifically, we contrasted each muscle mass with standard length using least-squares regression. Since mass increases dimensionally as the cubed function of length, we fitted an exponential curve to each data set for each species. We also wanted to compare the resulting relationship between species. However, the datasets do not overlap sufficiently in terms of TL. Therefore, direct comparison of curve parameters for each species may be misleading because the nature of the growth function may differ between intra- and interspecific size-classes. It is possible that for the morphological variables quantified here, *Girella* are equivalent to small *Graus*. In other words, the two datasets taken together would seem as one continuous set with a larger size range. To evaluate whether the muscle growth relationships for the two species were indeed different, curves were also fitted to the combined dataset, and the  $r^2$  was used to infer whether there was one relationship (using the combined dataset) or two (using species-specific datasets). Moreover, we tested for differences in muscle mass with size between species using an analysis of covariance (ANCOVA) approach to compare species-specific slopes fit to  $\log_{10}$  transformed data. In this model, species was a main effect (fixed) and TL was the covariate (SPSS 16.0).

We also contrasted the ratio of in-lever to out-lever for both jaw opening and closing with TL. This ratio is dimensionless and therefore should be constant with respect to length. The means, however, should vary among species if there are differences in force producing ability. High lever ratios reflect slow, forceful movements, while low lever ratios indicate rapid but weak movements. A Student's *t*-test was used to determine whether the mean lever ratios for both opening and closing were different between species (SPSS 16.0).

Finally, we examined additional specimens of *Girella nigricans* (from California) that were both fresh (frozen) and cleared and stained to better understand the architecture of the IMJ and associated musculature and the nature of potential movement at this joint during feeding. The left lower jaw of one specimen was completely dissected out, the bones cleaned using dermestid beetles and laser-scanned using a microscan30 via Microscan Tools v. 1.1.27 (RSI, Oberursel, Germany). The 3D scans of each bone were processed in Geomagic Studio v. 11 (Geomagic, Research Triangle Park, NC, USA), and rendered in Maya v. 8.5 (Autodesk, San Rafael, US). The anatomical results will be discussed first, to place the scaling and lever results into a larger context.

## RESULTS

### IMJ Morphology and Myology in *Girella*

The IMJ in *Girella* consists of a pin-joint between the posterior aspect of the dentary bone

and the distal-most ventral face of the articular bone (Fig. 1A). When manipulated, flexion at this joint (Fig. 1B) attains approximately  $20^\circ$  even though it appears to be dampened by connective tissue enveloping the bony articulation. Lower jaw depression, around the ancestral lower jaw joint (Fig. 1C) further depresses the tip of the lower jaw.

The jaw depressor and adductor musculature of *Girella* (Fig. 2) show some modifications relative to a generalized acanthopterygian (Winterbottom, 1974): The geniohyoid (GH; Fig. 2C) and AM section 1 (AM1; Fig. 2D) retain generalized insertion points and seem to have antagonistic lines of action when the articular is in resting position (i.e., jaws closed; Fig. 2A). Therefore, these muscles may govern IMJ flexion during lower jaw depression (Fig. 2B,C) and adduction (Fig. 2D), respectively. The AM section 2 (AM2; Figs. 2D and 3) inserts wholly on the posterior face of the dorsal articular aspect (Fig. 1), whereas the AM section 3 and w are fused (AM3,w) and insert medially on the dentary (Fig. 2C). Although the line of action of the AM2 suggests that it is the main section responsible for oral jaw closure (Fig. 2D), the function of the AM3,w complex is ambiguous. When the line of action of this AM complex falls below the IMJ fulcrum, i.e., when both the lower jaw articulation (LJA) and the IMJ begin to depress (Fig. 2B,C), this complex could function as an IMJ opener. However, this AM complex can still act as an IMJ closer when the dentary is already depressed, bringing the line of action of this AM complex closer to  $45^\circ$ , ergo, it would close the lower jaw with the IMJ in depressed conformation.

Possibly, this muscle section is required to keep the jaws in an optimal position for scraping during jaw closure, particularly given that the IMJ is encapsulated in connective tissue sheets, which might restrict the joint movements. Synchronized collection of high-speed video of feeding kinematics and electromyography from all AM sections in *Girella* will be required to determine the exact function of the respective muscle activity patterns.

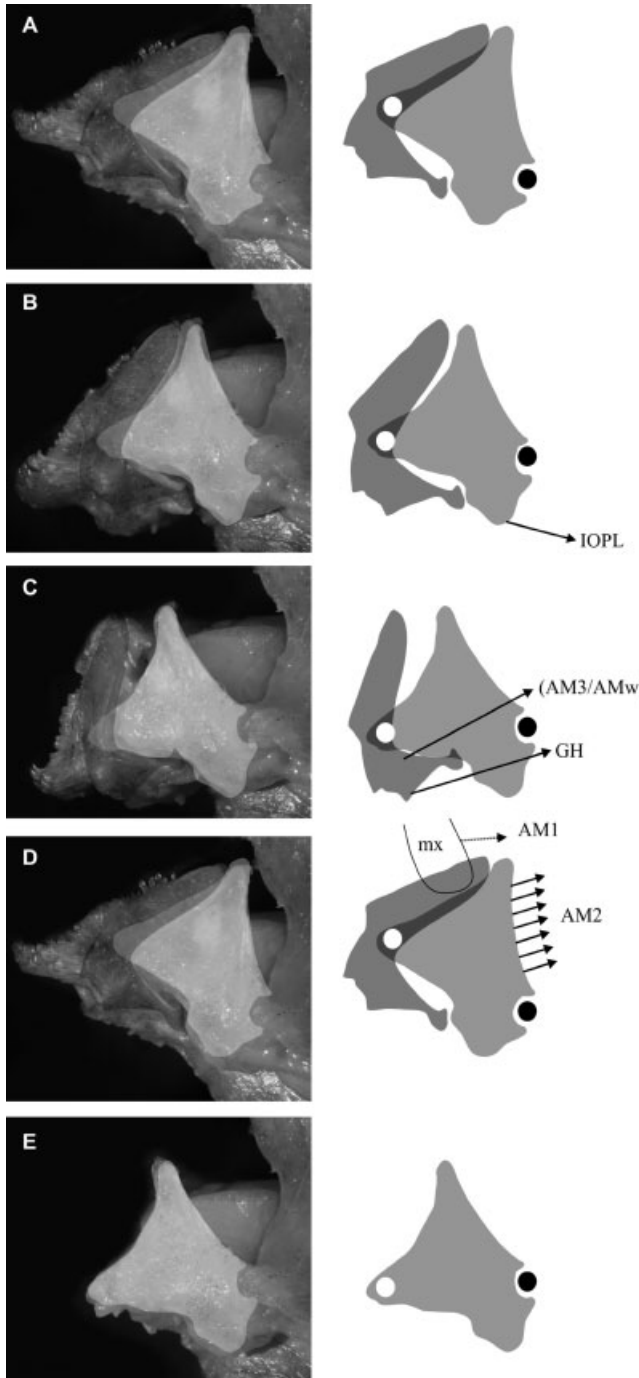


Fig. 2. Stepwise manipulation of dissected lower jaw in *Girella*, matching distinct kinematic events in Supporting Information video. Preopercular and maxillary bones, as well as the AM complex and the geniohyoid muscle, are removed. Superimposition of shaded outlines in the right column onto structures in column the left are for enhanced clarity. **A:** Resting position with the dentary tooth-bearing surface facing left and up. Black dot is lower jaw articulation (LJA) and white dot is intramandibular joint. **B:** Lower jaw depression, via IOPL (Fig. 3). **C:** Intramandibular joint flexion, via GH, and possibly AM3/AMw. **D:** Lower jaw retraction, via AM2, followed by intramandibular joint return-rotation, via AM1; **E:** dentary only.

### Scaling of Muscle Masses in *Girella* and *Graus*

When plotted against TL, both SH muscle mass and AM2 muscle mass increased exponentially (Fig. 4). As expected, the exponential curve applied provided a better fit, as determined by  $r^2$ , than linear or second polynomial curves. In the case of SH mass, the data for both species seem to be described better by one line ( $r^2 = 0.91$ ), as opposed to two lines for the two species ( $r^2 = 0.85$  and  $0.82$ , respectively). This suggests that the SH does not change shape substantially between species,

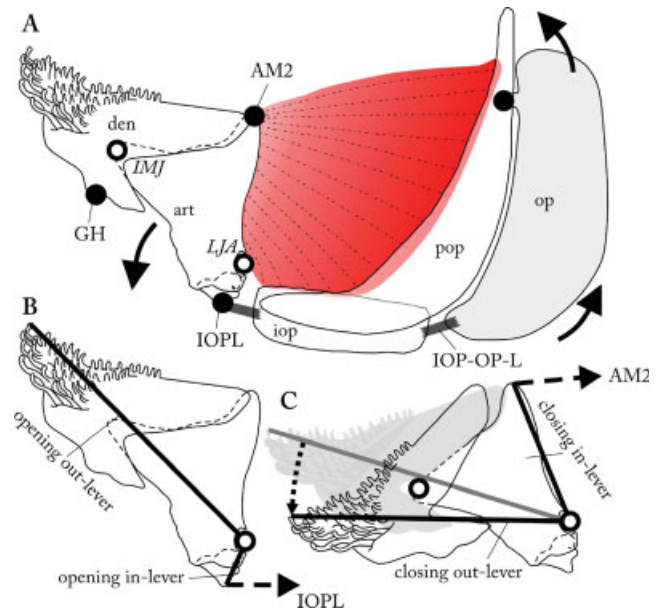


Fig. 3. **A:** Schematic of lower jaw morphology in *Girella*. Specific areas of interest in this study are indicated by circles. Note that the lower jaw articulation (LJA) is partly obscured by the AM2. The lower jaw is depressed by translation of force from the contracting SH and GH muscles and via opercular linkage rotation (top curved arrow) through the IOPL and IOP-OP-L. **B:** Opening in- and out-levers diagrammed on a schematic of the lower jaw in *Girella*. The IOPL attaches to the posterior ventral edge of the angular-articular. The distance from insertion of the IOPL to the articulation of the lower jaw with the quadrate (circle) is the opening in-lever. **C:** Closing in- and out-levers; the AM2 attaches via a tendon to the posterior aspect of the articular, and AM2 contraction rotates the IMJ back to relaxed position. The distance from insertion of the AM2 muscle to the articulation of the LJA is the closing in-lever. The distance from the LJA to the anterior tip of the lower jaw is the out-lever arm, which in generalized taxa remains equidistant during jaw opening and closing. However, note that this distance changes for the jaw closing out-lever measurement in *Girella* due to the IMJ (see also Vial and Ojeda, 1990). Abbreviations: AM2, section two of the adductor mandibulae muscle; art, articular; den, dentary; GH, insertion of the geniohyoid muscle (not shown); iop, interoperculum; IOPL, interopercular-mandibular ligament; IOP-OP-L, interopercular-opercular ligament; IMJ, intramandibular joint; LJA, lower jaw articulation; op, operculum; pop, preoperculum. [Color figure can be viewed in the online issue, which is available at [www.interscience.wiley.com](http://www.interscience.wiley.com).]

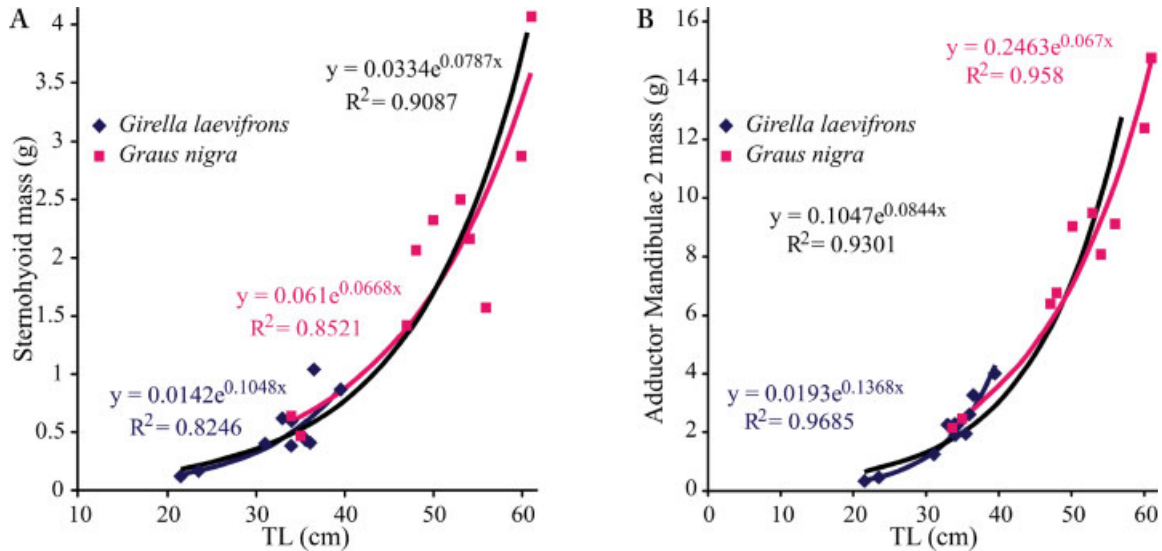


Fig. 4. **A:** Sternohyoideus muscle mass, and **B:** AM 2 muscle mass plotted against fish TL. The equation and fit of each curve is shown next to the line: *Girella* in diamonds, *Graus* in squares. The fit for the two datasets combined is shown in black. [Color figure can be viewed in the online issue, which is available at [www.interscience.wiley.com](http://www.interscience.wiley.com).]

and *Girella* are effectively just smaller *Graus* in this regard (Fig. 4A): a finding supported by the ANCOVA model comparing log-transformed values between species ( $F = 0.22$ ;  $P = 0.64$ , full model  $r^2 = 0.93$ ). However, for the AM2, the fit for the single line, albeit convincing, is worse than the fit for either species-specific line ( $r^2 = 0.93$  vs. 0.97 and 0.96, respectively); surprising, because an increase in sample size alone ought to improve the fit of a model. Therefore, there seem to be slight species-specific differences in the growth of the AM2 muscle (Fig. 4B), although these were not detected by the ANCOVA model performed on log-transformed values ( $F = 0.47$ ;  $P = 0.50$ , full model  $r^2 = 0.98$ ). Small *Girella* tend to have smaller AM2 masses than same-sized *Graus*, whereas large *Girella* tend to have larger AM2 masses than the same-sized *Graus*. However, this trend ends abruptly because *Graus* TL far exceeds the lengths attained by *Girella*, and accordingly, *Graus* ultimately achieves much larger AM2 masses.

### Relationship Between Jaw Lever Ratios and IMJ

The jaw opening lever ratio averaged 0.32 for *Girella* and 0.26 for *Graus* across individuals, i.e., significantly greater in *Girella* than in *Graus* ( $t_{2,18} = 5.96$ ,  $P < 0.0001$ ; Fig. 5). The closing ratio for *Girella* averaged 0.70, compared with 0.37 in *Graus*. These differences were also highly significant ( $t_{2,18} = 18.19$ ,  $P < 0.0001$ ; Fig. 5). This did not factor in the increase observed in closing lever ratio when flexion at the IMJ was taken into account. Effective shortening of the lower jaw in

*Girella* resulted in a significant increase in closing lever ratios ( $t_{2,18} = 6.82$ ,  $P < 0.0001$ ; Fig. 5) to a mean of 0.87, with values approaching 1.0.

### DISCUSSION

The IMJ in *Girella* appears to increase the gape-expansion capabilities, as previously shown in other species (Konow et al., 2008; Gibb et al., 2009). This function should maximize contact with the substrate thereby enhancing herbivory. Such enhancement of feeding ability seems a logical corollary of feeding on structurally and physiologically challenging prey such as marine algae (Clements and Choat, 1997). Although the mechanical approach of modeling of the jaws as levers simplifies what is truly a complex mechanical system of flexion (Konow and Bellwood, 2005), it illustrates that an increase in force production during jaw closure inevitably results from intramandibular flexion (Konow et al., 2008). This is an interesting example of how the functional innovation of an IMJ serves to channel the evolution of a novel feeding method, which is simultaneously constrained by the biophysical challenges of the feeding substrate. The key features driving the evolution of this system most likely include an increased control of the contact with the substrate via an increased and motile gape and an increase in force production during jaw closure. Importantly, this duality of mechanical function offers an alternative to the typically inherent trade-off between the force and velocity properties of an engineering mechanical system. To date, such a solution has only been described for two other feeding

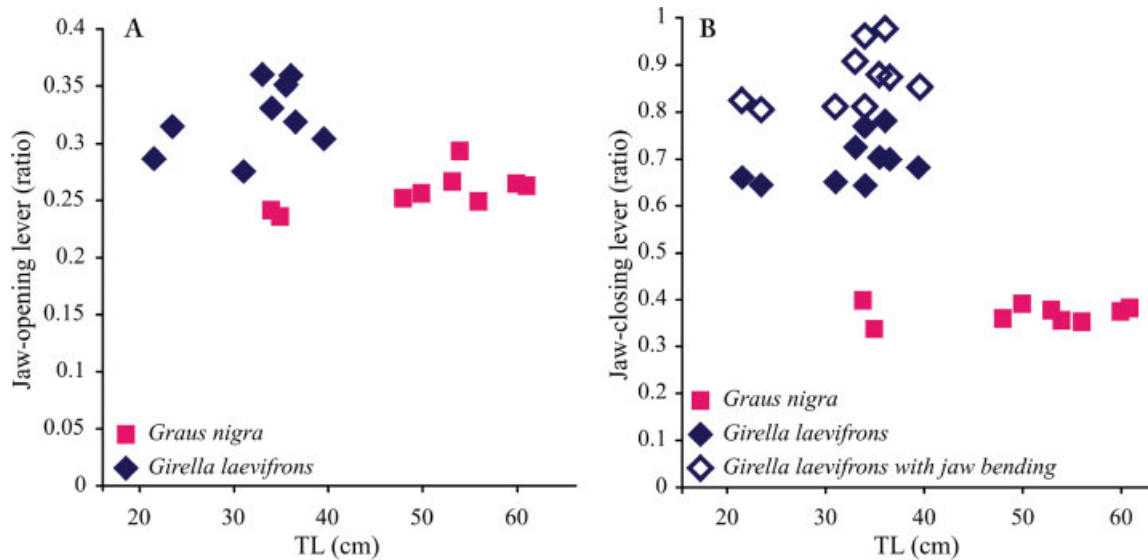


Fig. 5. **A:** Jaw opening and **B:** Jaw closing lever ratios plotted against fish TL. *Girella* in diamonds, *Graus* in squares. *Girella* with jaw bending incorporated into the model is shown in open symbols. Models with no jaw bending are shown in filled symbols. [Color figure can be viewed in the online issue, which is available at [www.interscience.wiley.com](http://www.interscience.wiley.com).]

systems, the extinct biting predator *Dunkleosteus terrelli* (Anderson and Westneat, 2007) and the Brook trout, *Salvelinus fontinalis* (Camp et al., 2009). Concomitantly, the IMJ results in an unavoidable loss in breaking strength of the lower jaw, since wherever flexion occurs, resistance to forces will be reduced. However, the placement of the flexion-moment effectively shortens the lever arm of the lower jaw. This increases jaw closing force and thus the forces transferred to the substrate for food removal and potentially countering the compromises in jaw strength.

Support for this argument is gained from studies of other IMJ-bearing taxa. The multiple origins of IMJs in parrotfishes have been linked with repeated transition from robust excavating or gouging feeding into more delicate scraping feeding habits (Streelman et al., 2002). Moreover, scraping parrotfishes generally have more gracile jaw elements than robust excavators (Bellwood, 1994). Similarly, a comparative analysis of two surgeonfish taxa suggested that the scraping habit corresponds with more gracile mandible bones and increased flexion at the IMJ thereby increasing the gape angle (Purcell and Bellwood, 1993). It is noteworthy that in most taxa with more pronounced IMJ flexion than in *Girella*, including the speciose parrot, surgeon, and rabbitfishes, the articular bone is significantly reduced in size. This reduction renders a relatively longer (larger) dentary bone, which moves the novel flexion moment closer to the ancestral lower jaw joint, thus amplifying the mechanical benefits of the IMJ (Konow et al., 2008).

Pomacanthid angelfishes are also IMJ-bearing biters, but kinematic studies of *Pomacanthus semicirculatus* suggest that the IMJ is used in an inverse fashion, to facilitate jaw closure while the jaws are still maximally protruded. This for example, permits spongivorous species to grip resilient, attached prey located in confined spaces and subsequently tear the prey off the substrate (Konow and Bellwood, 2005). Although this is a novel use of the IMJ, it still supports the idea of a transition to more kinetic jaws, in association with both biting behaviors and acquisition of an IMJ.

In contrast, *Graus* lacks such a joint, however, it consumes at least some herbivorous food during some portions of its life cycle (Johnson and Fritzsche, 1989). Our findings suggest that a forceful bite, as required to prey on tough, rubbery algal food, may be generated in *Graus* via the hypertrophied AM2 muscle. Still, the jaw mechanics in *Graus* theoretically prevents a forceful scrape *en par* with that measured for *Girella*. The trend of muscular hypertrophy and increased robustness of bony elements is mirrored in gouging and excavating scarids (Tedman, 1980; Bellwood, 1994; Alfaro and Westneat, 1999; Streelman et al., 2002) and in the Tetraodontiformes (Friel and Wainwright, 1997). Possibly, *Graus* relies more strongly on a gouging feeding mode, a question that can only be effectively answered via kinematic study of live animals. However, previous studies do indicate that a general relationship exists between robust jaw morphology and gouging or excavating habits (Purcell and Bellwood, 1993; Alfaro and Westneat, 1999; Streelman et al., 2002), particularly with

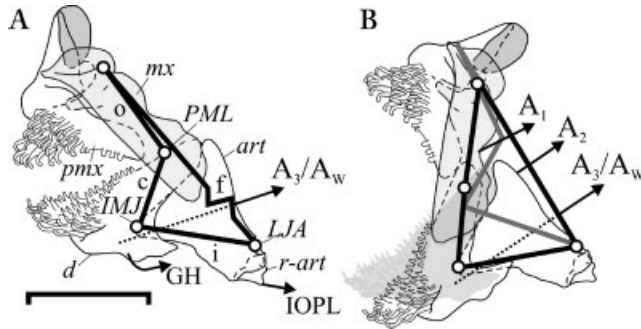


Fig. 6. Mechanical hypothesis of gape-expansion and occlusion in *Girella* using a four-bar linkage model to explain fluctuations in the force and velocity production of the IMJ-bearing jaw system. **A:** Ligaments limit upper jaw protrusion so that the mx-pmx complex rotates and protrudes anteroventrally due to four-bar rotation around the IMJ caused by the GH muscle, simultaneously with mandible rotation around the LJA (Fig. 3). Note shortening of the four-bar fixed link, presumably due to flexion in the palatoquadrate, which accelerates output angle rotation (see text). **B:** Mandible adductor insertions serve to retract the upper jaw complex, rotate the dentary back around the IMJ (AM1), and occlude the oral jaws (A2, AM3/AMw). Note that the degree of dentary depression theoretically is reduced, and the jaw-gape is diminished, when IMJ flexion is omitted (shaded dentary element, see also Fig. 3). Labeling—four-bar: f, fixed link; c, coupler link; i, input link; o, output link. PML, primordial ligament, connecting the maxilla (mx) and dentary (d) bones; IMJ, intramandibular joint, joining the dentary and articular (art) bones; GH, geniyoideus muscle lines of action; A1, adductor mandibulae section 1; A2, section 2; A3, section 3; Aw, section w; r-art, retro-articular; pmx, premaxilla.

respect to muscle force generation (Alfaro and Westneat, 1999).

Having addressed the functional ecological role of IMJ flexion during jaw closure, the questions then arise: how is the IMJ flexion achieved and how does it function during the gape-expanding phase of biting in *Girella*? We close our discussion by putting forth a working hypothesis: a four-bar planar linkage model that potentially explains IMJ function in *Girella* and other IMJ-bearing biting fishes. This engineering principle has successfully been used to quantify the role of, for example, opercular elevation in driving mandible depression and the role of mandible depression in driving upper jaw protrusion (Aerts and Verraes, 1984; Westneat, 1990; Westneat, 2004). In this IMJ four-bar model (Fig. 6), the fixed link (f) is the palatoquadrate complex, spanning from the ancestral lower jaw articulation (LJA) with the palatine-maxillary articulation. The output link (o) is the maxillary from its palatine articulation to the midpoint of the sturdy primordial ligament (PML), which joins this out-lever bone (mx) with the dentary (d). The coupler link (c) spans from the coronoid to the IMJ, from where the input link (i) reaches the LJA. In the ancestral mandibular morphology, the lower jaw is depressed via shortening of the SH, which pulls on the hyoid bar and the GH, which connects the hyoid bar to the lower

jaw. However, in the derived IMJ-bearing mandible, GH shortening (and possibly shortening of the AM3,w section) causes rotation of the dentary bone around the distal end of the articular bone (art) at the IMJ. This rotation augments gape-expansion, and by virtue of occurring along with lower jaw depression (around the LJA), the velocity of gape expansion is amplified. Moreover, when kinematic and force transmission coefficients are calculated for the four-bar (using a measured input angle and the laws of sine and cosine; Camp et al., 2009), the four-bar linkage transmission coefficient shifts toward a velocity-modified system ( $KT = 2.19$ ), as opposed to a force-modified system ( $FT = 0.46$ ). The combined result is an overall amplification of lower jaw depression and gape-expansion speed.

Conversely, during oral jaw closure, the closing out-lever is shortened by the third-order lever system, as explained above (Fig. 3). Initial video evidence from *Girella* (Supporting Information video) suggests that the IMJ remains bent during most of the biting power stroke to keep the tooth-bearing surface engaging the feeding substratum (*sensu* Konow et al., 2008), and thus the four-bar input-link remains shortened. During jaw closure, the input comes from the mandible adductor musculature attaching to the articular (AM2) and the maxilla (AM1; Fig. 6B). Because the line of action of the AM3,w rotates above the IMJ fulcrum during the concluding part of the bite, this section might control the final closure of the jaws by rotating the dentary tooth surface dorsally. This lengthening of the lower jaw out-lever would result in a final element of velocity increase to the occlusion of the oral jaws, thus instating a speed-modified system, possibly serving to dislodge robust and sturdily attached prey such as macroalgae. This hypothesized functional duality of mechanical lever and linkage systems during the inverse jaw motion phases (depression/expansion and elevation/occlusion) represents a novel, albeit still insufficiently studied, biological system. The complex mechanical function may adequately explain how a gracile skeletal construction is capable of generating the force, followed by the velocity required to dislodge diverse types of attached reefal benthos.

Our model builds on a “modified anterior four-bar” of Van Dobben (1935), which was reproduced by Wainwright et al. (2004). As pointed out by Muller (1996), this four-bar model cannot power-amplify. Therefore, we assume that the conclusions reached about power amplification in scarids by Wainwright et al. (2004) were based on calculations using the jaw closing lever model. Herein, we present quantitative evidence suggesting that the power-amplification of the scarine IMJ-bearing jaws might be better explained using single lever mechanics than a four-bar linkage. However, it is important to note that both these mechanical mod-

els remain untested hypotheses from a functional perspective. Studies are underway to compare the utility of these models in explaining different IMJ functions, such as the gape occluding mechanisms in pomacanthids versus the gape-expanding mechanisms in all other known IMJ bearers (Konow and Bellwood, 2005; Konow et al., 2008). Here, we conclude that single-lever mechanics offer a solid explanation of the force amplified bite in *Girella*.

In summary, we used mechanical models to corroborate our theory that the IMJ, as seen in *Girella*, is a mechanism that both from a mechanical and a physiological perspective facilitates scraping herbivory. This may be achieved via two mechanisms that function complementarily to ultimately increase the force production during mouth closure, thus increasing the force exerted onto the substrate to which food items are attached. This may be a secondary advantage of a mechanism that initially evolved to rapidly open the mouth while optimizing and increasing the amount of contact between the teeth of the oral jaws and the substrate. Nevertheless, this novel functional system fits within the suite of changes observed in herbivorous fishes associated with increased force production for prey acquisition.

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