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Lateral jaw motion in fish expands the functional repertoire of vertebrates and underpins the success of a dominant herbivore lineage

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The primary function of the vertebrate jaw is the dorsoventral movement that occurs during opening and closing. Yet, several lineages have evolved the ability to move their jaws laterally, enabling major innovations, like chewing. While lateral jaw motions are primarily known in tetrapods, here, we show that an ecologically dominant lineage of reef fishes (Zanclidae and Acanthuridae) has evolved the ability to laterally rotate their jaws during feeding. This unique function substantially expands both the kinematic versatility and known diversity of vertebrate jaw mechanisms, adding to the growing list of innovations that followed the origin of jaws. Within Acanthuridae, this increased kinematic versatility may allow for algal detachment with minimal movement of the rest of the body, facilitating rapid biting within the same microtopographic location, and thus, this lineage having the highest bite rates among biting reef fishes. This innovation may have thus helped create one of the most ecologically diverse and speciose herbivorous reef fish lineages. Our results highlight the ecological and evolutionary impact of lateral jaw rotation within vertebrates, and potentially how this novelty led to a significant change in coral reef trophodynamics.

coral reefs | morphology | ecosystem function | evolutionary innovation | herbivory

Feeding-related innovations have been pivotal to the success of vertebrates. For example, the evolution of a jaw in gnathostomes about 443 to 433 Mya (1, 2) was a key step toward the vast array of additional novelties in the feeding mechanism that are used in a huge range of ecological contexts (3–5). To this day, the relatively simple dorsoventral motion for mouth opening and closing that arrived with the first jaws is a primary component of vertebrate feeding mechanisms.

In contrast to the typical dorsoventral axis of jaw movement, some vertebrate groups have evolved the ability to generate side-to-side (i.e., lateral) jaw motions during feeding, a prominent example being chewing in tetrapods. The ability of tetrapods to chew with the mandible led not only to an increase in the types of food that could be efficiently eaten (6–8), but also, altered the nature of terrestrial communities by contributing to key ecosystem processes such as herbivory in mammals (9). In a second example, snakes have the ability to spread their jaws laterally at the symphysis (10), thus significantly increasing the size of the mouth opening. This novelty along with other morphological characteristics resulted in snakes changing the nature of trophic interactions (e.g., ingesting larger prey) with cascading impacts on terrestrial ecosystems (11, 12). Recently, mediolateral movement of the mandible in certain finches (Fringillidae) was linked to an increased performance in seed processing (13, 14), another organismal function of crucial importance to broader ecosystem processes (15). Taken as a whole, the evolution of lateral jaw movement in various vertebrate groups has been central to ecological expansions that have changed the nature of terrestrial ecosystems. Whether similar functional innovations in lateral jaw movement have occurred in the aquatic realm, where most vertebrate diversity is found, has remained relatively unexplored.

Actinopterygian fishes represent about half of extant vertebrate species (16). They have evolved a vast array of innovations that provide access to some of the most specialized niches worldwide and can be found in most aquatic habitats on our planet. Many of these innovations support benthic association and feeding, a highly influential ecological transition that has resulted in extended periods of success for many of the groups involved (17–19) and contributes to key ecosystem processes, especially on hyperdiverse contemporary reef systems (20–22). It is therefore essential to understand the morphological, mechanical, and behavioral drivers of these ecological expansions if we are to understand

Significance

When similar lateral (side-to-side) jaw motions evolved in other vertebrate lineages, it led to major species diversification and broad-scale ecological change within these habitats. Within *Zanclus* (simultaneous rotation of both jaws), this functional innovation represents an example of lateral jaw motion within ray-finned fishes, which make up about half of vertebrate species. Furthermore, a modified version of this innovation is found in the Acanthuridae (rotation of the upper jaw), a major herbivorous fish lineage that uses this function to crop algae with increased dexterity, facilitating some of the highest bite rates within benthic-feeding reef fishes. This innovation may therefore have been a spark in igniting the ecological and evolutionary success found in this group of functionally important reef fish.

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the evolutionary history of actinopterygian fishes, and how they function within ecosystems.

One major class of innovation in actinopterygian jaws encompasses anatomical changes that allow variation in jaw mobility, with increasingly complex movements supported by the evolution of novel joints. Most of these motions occur in the parasagittal plane (i.e., anteroposterior axis) of the body. A primary example is the intramandibular joint (23–25), which allows species to flex their lower jaw, and produced new niche access due to novel mechanical interactions with benthic prey (26). Another example is upper jaw protrusion, made possible by a premaxilla that is no longer fused to the skull. Upper jaw protrusion increases the suction ability of fishes (27), and again, allowed species to specialize and diversify along new ecological axes (e.g., ref. 28). There are also several examples of novel joints forming in the cheek bones that allow the entire jaw apparatus to be protruded anteriorly, sometimes to extreme lengths (29–31). Furthermore, cranial rotation through the craniovertebral joint, an essential component of powerful suction feeding (e.g., ref. 32), is used by some benthic-feeding lineages to dislodge prey held in the closed jaws (33). One feeding-related motion in the lateral direction that occurs widely in actinopterygian fishes, is the bilateral buccal expansion that occurs during suction feeding (e.g., refs. 34, 35). This bilaterally symmetrical motion relates to multiple bones in the head, that expand laterally when producing the volumetric increase of the buccal cavity seen in most suction feeding taxa. Unilateral motion is seen in a scale-eating cichlid and flatfishes; however, in these instances, the lateral motion is caused by skeletal asymmetry, which constrains jaw motions to be directed away from the midline (36, 37). Other jaw-related motions occurring laterally during feeding have rarely been observed in actinopterygian fishes.

Here, we show a dramatic departure from this trend, with the ability of an actinopterygian reef fish, *Zanclus cornutus*, to generate substantial lateral rotation of both its upper and lower jaws simultaneously, permitting the fish to bend the jaws laterally toward its prey during bouts of benthic feeding. Furthermore, we show that a modified version of this mechanism is also present in the sister group of *Zanclus*, the surgeonfishes (Acanthuridae), a diverse and highly successful lineage of mostly benthic-feeding reef fishes. In both cases, the movements appear to be actuated by asymmetric contraction of jaw adductor muscles that pull the jaw to the side of muscle contraction, allowing lateral jaw motion and various phases of normal jaw movement. Our multimethod approach provides 1) a detailed understanding of this morphological and kinematic novelty, revealing an example of lateral flexion of the upper and lower jaws in any actinopterygian fish (*Z. cornutus*), and 2) a comprehensive description of upper jaw rotation within Acanthuridae, as well as how it is used in extracting and manipulating attached algae, a crucial ecosystem process in reef systems. Our results support the hypothesis that lateral jaw rotation in surgeonfishes may be a major factor underlying their high bite rates that helps make them one of the ecologically and evolutionarily most successful biting reef fish lineages on modern reefs.

Results and Discussion

Through anatomical dissections, micro-CT scanning, and high-speed filming in both the lateral and anterior view, we show that *Z. cornutus* can simultaneously flex both its upper and lower jaws laterally (Fig. 1 and Movie 1). Furthermore, we show that a modified version of this mechanism is found throughout surgeonfishes (Acanthuridae), the sister lineage of Zanclidae. While *Zanclus* can rotate both jaws simultaneously, surgeonfishes were found to only rotate their upper jaw. *Z. cornutus* rotates the lower jaw (dentary and articular bones), and upper jaw (maxilla and premaxilla bones), with a total range of 51.8° (25.9° away from the midline, toward either side). This motion contributes about 36% of the distance covered during a bite by the jaw tips, relative to when the jaws open and close (i.e., dorsoventral motion). This represents an example in actinopterygians of lateral motion of both the lower and upper jaws, a previously unknown jaw function within vertebrates. This novelty significantly increases the kinematic versatility (range of motion capabilities and degrees of freedom) of *Z. cornutus*, which the species capitalizes on when feeding in structurally complex reef habitats that have many benthic resources with different extraction requirements. To explore the mechanisms and functional implications of these kinematic novelties for both lineages (Zanclidae and Acanthuridae), we conducted a high-speed filming study across reef fish lineages that use biting when feeding on benthic prey.

Lateral Jaw Rotation in Acanthuridae Underpins Algal Detachment. Based on 674 high-speed videos by 65 individuals from 35 biting species from 10 major biting reef fish families, we show that lateral jaw rotation is used by *Z. cornutus* and most species within the Acanthuridae (Fig. 2). Lateral jaw rotation was not observed in any of the eight other families of benthic-feeding reef fishes that were filmed. All acanthurid species but three exhibited lateral rotation of their upper jaw, either when detaching filamentous algae (Fig. 2 and Movie 2), or when processing algae that had already been detached. The exceptions to this pattern were *Ctenochaetus strigosus*, as species within *Ctenochaetus* are known for their specialized detritivory through a scraping feeding mode (38), and two sister species (*Acanthurus leucosternon* and *A. japonicus*), which crop algae through ventral jaw motions as opposed to lateral (33). We did not observe any intraspecific variance in the presence or absence of this jaw motion, meaning that, if a species possessed the ability to conduct lateral jaw rotation, it was recorded in all individuals within that species.

Unlike *Zanclus,* which rotates its jaws as it approaches the substrate (Fig. 3), surgeonfishes rotate their upper jaw laterally after they bite filamentous algae and as they initiate a lateral movement of the head, sometimes culminating in a sideways headflick (see Fig. 4 and Movie 3), highlighting that this kinematic novelty is tightly linked to resource detachment. We note here that while simultaneous lateral rotation of both upper and lower jaws appears to be unique to *Z. cornutus* across actinopterygians, lateral motion of the upper jaw has been postulated in a benthic feeding cichlid (*Petrotilapia tridentiger*) (39). This suggests that while the function of a rotating jaw for *Zanclus* may have been for increased kinematic versatility when feeding in crevices, it found a different function among surgeonfishes, increasing the dexterity of the jaws, providing subtle but effective movement when breaking small algae filaments. This increased dexterity may have been important for feeding on different algal resources within turfs, or areas with varying topographic features (e.g., vertical or concealed surfaces), something surgeonfishes are well known for (40–43). On reefs, algal turfs are highly diverse communities consisting of a large variety of species, morphotypes, and growth forms (44–46). There have been multiple categorizations of these turfs, such as filamentous, foliose, and thallate to describe different structural categories (40, 47). This diversity of structures within turfs may require different types of force applications and small, subtle motions to efficiently detach them (e.g., sideways forces, biting at a specific part, or at a specific angle).

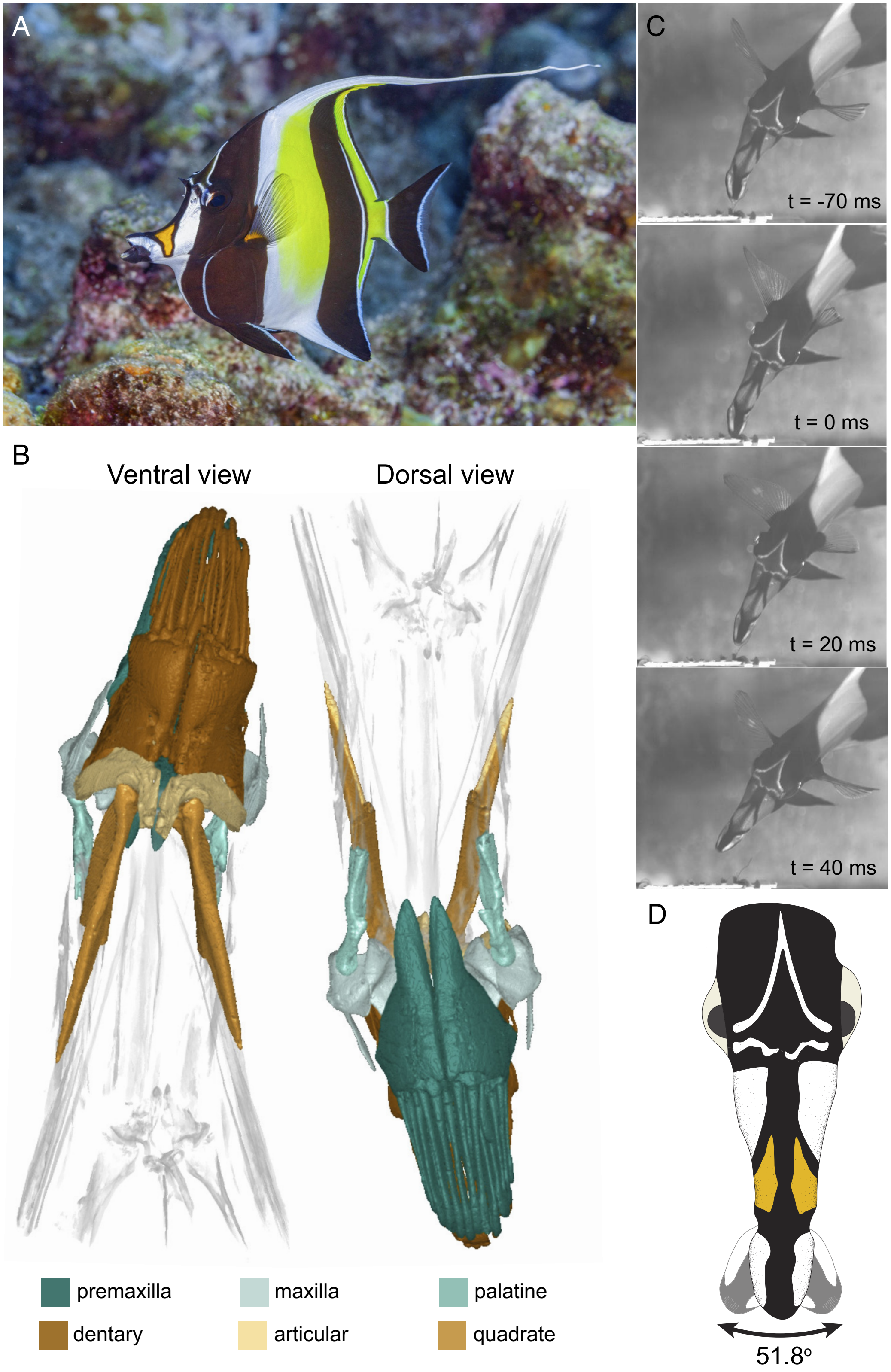

Fig. 1. The morphological innovation of *Zanclus cornutus* and its ability to rotate its jaws laterally. (*A*) shows an individual *Z. cornutus* photographed in the wild (credit: Victor Huertas), and (*B*) shows ventral and dorsal views from CT scans of *Z. cornutus*, with the different bones color-coded. (*C*) Frames from a bite sequence recorded of *Z. cornutus* feeding on a benthic resource. Time zero (t = 0) represents the time at which the jaws contact the substratum. (*D*) shows the maximum range of jaw rotation from our videos.

We suggest this lateral jaw motion provides a significant performance benefit for cropping short filamentous algae, the most abundant benthic resource on coral reefs (48). Our results show that lateral motions of the upper jaw are particularly observed during algal detachment (Fig. 4), and substantially increase the kinematic versatility these species are able to deploy. Underlying these novel jaw movements in surgeonfishes, we highlight anatomical novelties, such as modifications of the adductor mandibulae muscles (see below: A detailed analysis of lateral jaw rotation in Acanthuridae, *SI Appendix*, Fig. S6). Lateral jaw motion appears

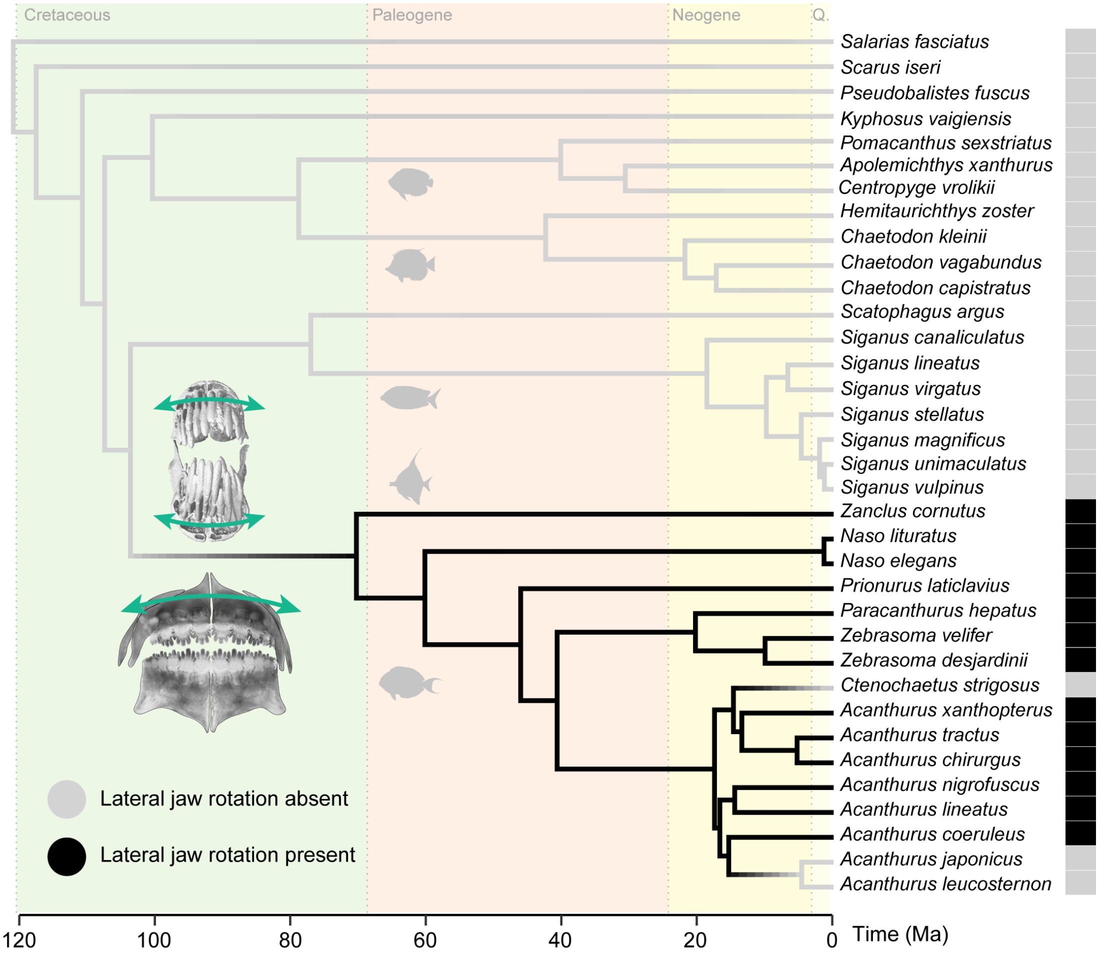

Fig. 2. Distribution of lateral jaw rotation across the species filmed. Phylogenetic tree with a mapping of lateral jaw rotation. The innovation was found in *Z. cornutus* and most of the Acanthuridae filmed. Squares to the right of the phylogenetic tree represent the presence (black) or absence (gray) of lateral jaw rotation.

to function in a manner that allows surgeonfishes to conduct a cutting action against algae they have bitten, in a way that minimizes the need to employ the whole body in a full lateral headflick. This jaw motion may also allow surgeonfish to conduct multiple bites while maintaining their position, without needing to reorient the body after a headflick, which would promote greater feeding efficiency. Such a morphological and kinematic novelty would likely have a substantial impact on the bite rates of this family, which could impact overall rates of herbivory, a crucial ecosystem function. We, therefore, conducted a meta-analysis of field observations to test this hypothesis.

Ecological and Evolutionary Implications of Lateral Jaw Rotation within Surgeonfishes. Surgeonfishes remove turf algae during feeding, thereby carrying out functions that influence ecosystem processes with important implications for the resilience of coral reefs (21, 49–51). Based on a meta-analysis with a total of 389 observations of bite rates across eight reef fish families that feed through biting, we show that Acanthuridae possess the highest average bite rates across all families analyzed (Fig. 5). Acanthuridae were found to have an average bite rate of 22.8 bites per minute (20.7 to 25.1, 95% CI), followed by Labridae (Scarinae) with 15.8 (14.3 to 17.4, 95% CI) (Fig. 5, for model details, see *SI Appendix*, Table S1). In other words, Acanthuridae were found to bite approximately 1.5× times faster than parrotfishes, the group with the second highest bite rate. We argue that the evolution of lateral jaw rotation within Acanthuridae, through its impact on algae cropping efficiency, likely underlies a significant increase in the amount and rate of herbivory occurring on coral reefs, and may be one of the keys to surgeonfish success on modern coral reefs.

Coral reefs are oligotrophic systems (52), with primary producers such as algae releasing substantial amounts of fixed carbon, of which up to 80% immediately dissolves in seawater (53, 54). Therefore, life-essential compounds such as carbon and nitrogen, are especially important within reef systems for the transfer of energy and nutrients through the trophic chain. An organismal innovation enhancing access to turf algae, the most abundant benthic resource (48, 55) likely significantly increased the energetic flux of carbon and nitrogen on Eocene reef systems when surgeonfishes emerged, at a time when few herbivorous reef fish were present (see also ref. 56). This dramatic change in feeding efficiency by herbivorous fishes likely altered the nature of reef trophodynamics (see refs. 57, 58) by changes to the fish community through increased competition, while modifying the benthic composition of reefs.

The independent evolution of lateral jaw motion in birds (13), reptiles (10), terrestrial mammals (8), aquatic mammals (59), chondrichthyans (60), and actinopterygian fishes, reveal that this innovation has had substantial ecological impacts (e.g., ref. 9). Within actinopterygian fishes, it appears to have supported herbivory within the Acanthuridae, one of the most ecologically diverse and speciose lineages of herbivorous coral reef fishes (41, 61). Much like terrestrial grazers shaping fire dynamics through their feeding (62), grazing reef fishes have far-reaching ecosystem influences on the benthic community composition of their system (20, 21).

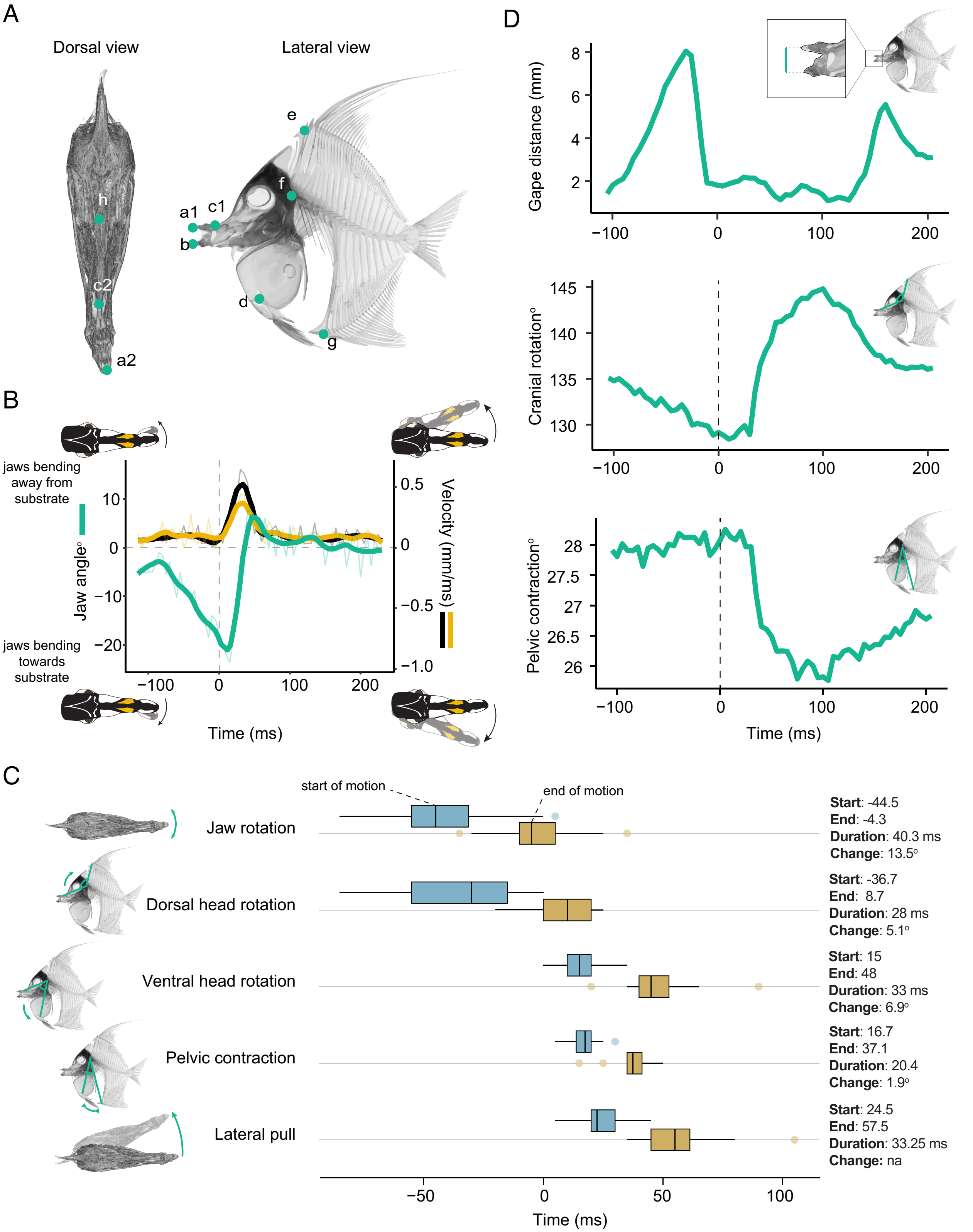

Fig. 3. Kinematic timeline of the key motions in a *Z. cornutus* bite. (*A*) shows the landmarks placed in the dorsal and lateral views. For a detailed description of the landmark definitions, see *SI Appendix*, Table S2. (*B* and *C*) show a representative bite of *Z. cornutus*. In (*B*), the *Left* y-axis represents the angle of the jaw relative to the rest of the body (based on landmarks h-c2-a2). A value of zero represents nonrotated jaws, negative values represent jaws rotated to the *Right*, and positive values represent jaws rotated to the *Left*. The *Right* y-axis represents the velocity of the anteriormost point of the neurocranium (landmark c2, shown in yellow), and the anteriormost point of the jaws (landmark a2, shown in black). (*C*) shows the time at which the different motions start (blue) and end (orange). Values for each motion on the *Right* are based on mean values from all the bites recorded and landmarked. For (*D*), gape distance is based on landmarks a1-b, cranial rotation on landmarks c1-f-e, pelvic contraction is based on landmarks d-f-g, and time = 0 represents the time at which the fish jaws contact the substrate. For data plot *B*), smoothed lines have been produced, with raw data shown in the background.

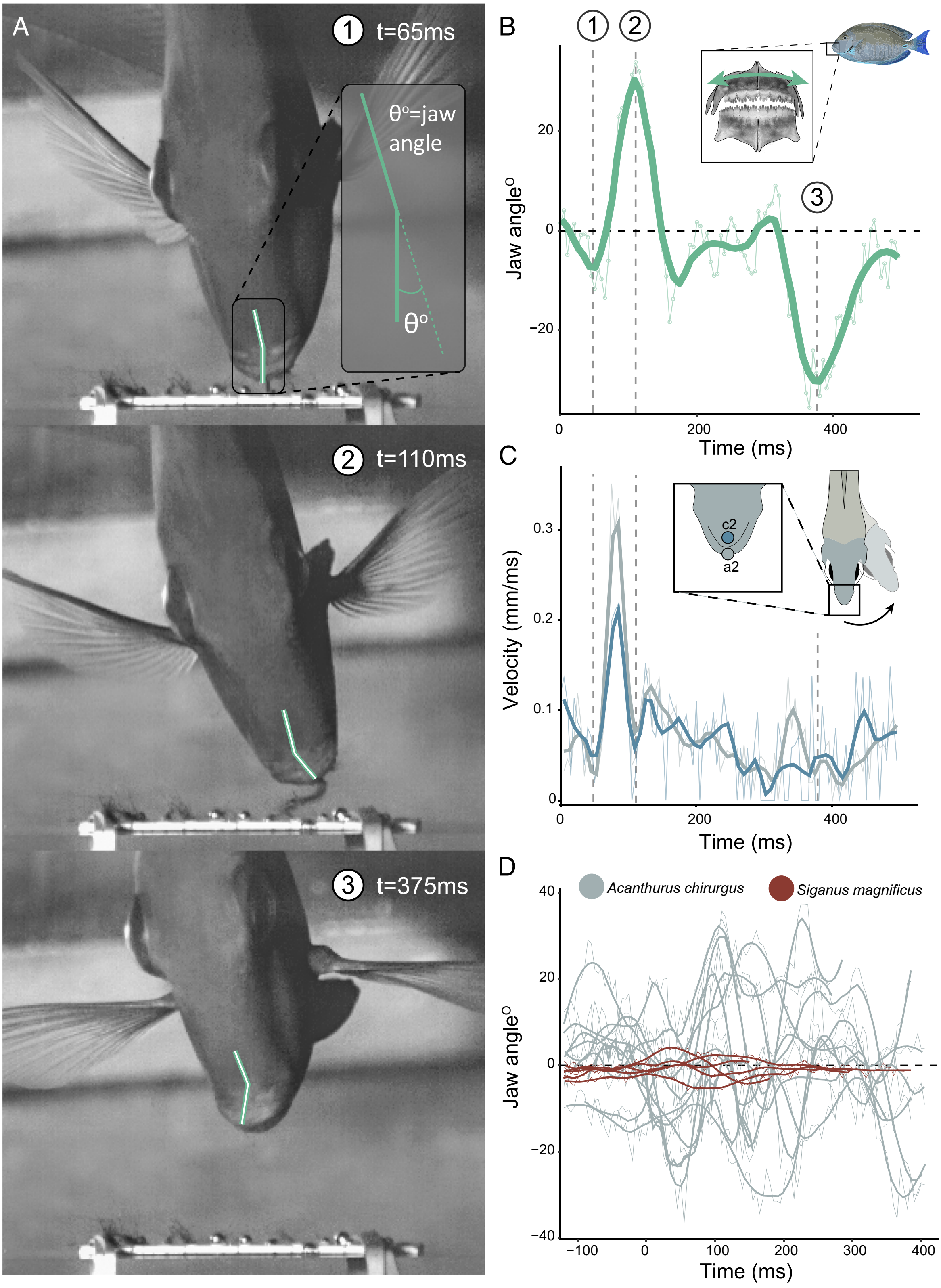

Fig. 4. Kinematic profile of a surgeonfish (*Acanthurus chirurgus*) bite. (*A*) shows lateral upper jaw rotation in a surgeonfish (*A. chirurgus*) throughout a bite sequence, where both jaw rotation and a head flick can be seen. The panels also show a representation of how jaw angle was measured throughout bite sequences from frontal view recordings. (*B*) Jaw angle for a bite by *A. chirurgus*. A value of zero represents no change to the angle between the jaws and rest of the head, whereas positive values represent jaw rotation to the *Left* side (observer's frame of reference), and negative values, rotation toward the *Right* side. Numbers in circles represent the jaw angle at a specific time of the bite (dashed lines), as well as the panels seen in (*A*). (*C*) represents the velocity of the jaws and head (based on landmarks a2 and c2 respectively) during the same bite depicted in (A) and (*B*). (*D*) Example of multiple kinematic profiles of jaw angle from a species with jaw rotation abilities (*A. chirurgus*), and one without (*Siganus magnificus*). Note the kinematic variability between bites from *A. chirurgus*, relative to bites by *S. magnificus*. For data plots, smoothed lines have been produced, with raw data shown in the background.

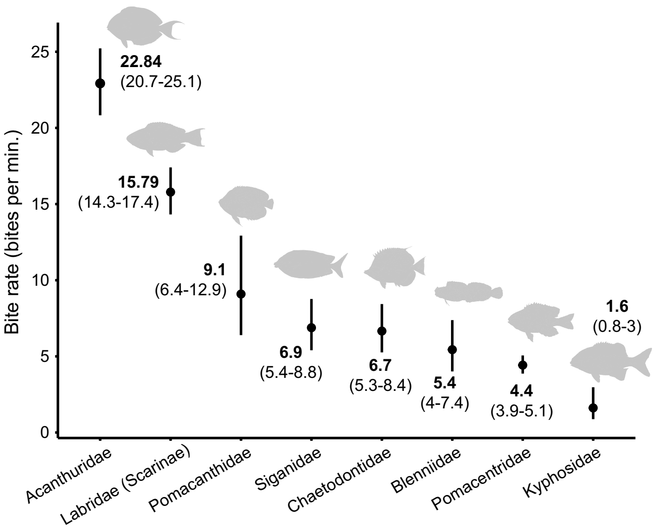

Fig. 5. Bite rates of benthic-feeding reef fish families. Results from a meta-analysis of observational studies of feeding rates in benthic-feeding reef fishes. The y-axis represents the number of bites recorded per minute, whereas the x-axis represents the different fish families. Values in bold represent the mean, whereas values in parentheses represent the 95% CI.

Although only rarely evolved, lateral jaw motion within vertebrates appears to have had substantial impacts in both the terrestrial and aquatic realms. While this novelty has gained considerable attention within the terrestrial realm with studies analyzing the mechanics of chewing (63–65), our results reveal a limited understanding of how this innovation works in the marine realm.

A Detailed Analysis of Lateral Jaw Rotation in *Z. cornutus*. High-speed video was recorded from both the lateral and dorsal views of individuals while they fed on benthic attached resources. These videos revealed that lateral jaw flexion takes place as the fish approaches the substratum, just prior to taking a bite (Figs. 1*C* and 3). Initial jaw flexion occurs toward the substrate, in the direction opposite to which the standard sideways head-flick used by biting reef fishes (including *Z. cornutus*) occurs (33, 66). This lateral motion is initiated on average 46.6 ms (± 5.1 SE) prior to the jaws contacting the substratum (defined as time = 0; Fig. 3). At time = 0, the angle between the jaws and the rest of the head is 6.8° (± 1.2 SE). At 10.2 ms (± 1.04 SE) after contact with the substratum, the fish initiates a pull on the prey through ventral rotation of the neurocranium, which lasts 15 ms (± 0.96 SE). In the anterior view this motion is observed as the fish's jaws and head moving away from the substratum, (see Fig. 1*C*, t = 20 ms). At 24.5 ms (±1.98 SE) after contact with the substratum, the motion transitions into a sideways pull which lasts 33.25 ms (± 3.17 SE) (Fig. 1*C*). During this sideways pulling motion, the jaws rotate back to their initial position and occasionally continue rotating past the midline to a few degrees in the direction away from the substrate (Fig. 3*B*).

Based on micro-CT scanning (Movie 3), dissections, and previous work on the myology of the species (67, 68), we identify several anatomical elements relating to this innovation. Zanclidae and Acanthuridae share a novel subdivision of the adductor mandibulae muscle, namely A1α, as well as partial fusion of A1β to the A2 muscle (67). Within Zanclidae (67), there are three morphological novelties that appear to relate to lateral jaw motions: 1) A1β inserts on the posterior edge of the maxillary blade, 2) new AM subdivision A3 attaches on the mandible, and 3) there is a double-headed articulation between the dentary and articular that permits some lateral bending at this joint. Based on our morphological dissections and CT scans, we describe and suggest three more.

The dentary bones are not fused or sutured at the symphysis but are held together by connective tissue fibers that permit considerable movement between the bones, allowing one dentary to slide anteriorly ahead of the other. This is a key feature of the jaw-bending mechanism. When the jaws are flexed laterally the articular and quadrate bones do not separate at either jaw joint. Instead, the left and right mandibles slide against each other at the symphysis with the one on the side to which the jaw is flexed extending ahead of the contralateral mandible (Fig. 1*B*). An unfused symphysis is also associated with lateral jaw motion in some other vertebrate lineages capable of lateral jaw movements, such as snakes (10), and some chondrichthyans (60). We note that lateral lower jaw motion in mammalian vertebrates is accommodated by the contralateral mandibular condyle sliding anteriorly in the temporomandibular joint, thus negating the need for an unfused symphysis between left and right mandibles. However, in *Zanclus* and Acanthuridae, the joint between the lower jaw and rest of the head, the articular-quadrate joint, does not permit the bones to move apart, and therefore, is unable to conduct the sliding motions found in mammalian jaws. The unfused symphysis appears to be a key component of lateral jaw motion for nonmammalian vertebrates.

The modified shape of the quadrate-articular joint (q-art) also functions prominently in lateral jaw rotation. Typically, in other actinopterygian fishes, the two condyles of the quadrate that make up the joint, are oriented so that only dorsoventral rotation of the mandible is allowed. However, in *Z. cornutus*, the two condyles are rotated about 45° so that the mandible rotates away from the midline when the jaw is abducted (*SI Appendix*, Fig. S2). An additional important anatomical feature is the shape of the maxilla. A protrusion on the distal end of the shaft of the maxilla, in addition to being an attachment point to functionally important ligaments (see Supplemental Text), is also situated along the dorsal part of the dentary. When the maxilla rotates in one direction, the maxillary protrusion of the opposing side may tighten the ligaments connecting to the dentary in the transverse plane (*SI Appendix*, Fig. S3). In other words, the modified maxilla shape may aid in transferring lateral jaw motion between the upper and lower jaws (*SI Appendix*, *Supplementary Text*). Overall, the *Z. cornutus* jaw system consists of several novel features, highlighting the complex nature of this innovation.

A Detailed Analysis of Lateral Jaw Rotation in Acanthuridae. Within Acanthuridae, there are multiple jaw-related anatomical novelties (67–69). All acanthurids have short jaws with vertically oriented teeth, strongly contrasting the anteriorly oriented teeth of *Zanclus*. In many acanthurids, the teeth are multicuspid, whereas *Zanclus*, like most actinopterygians, have unicuspid teeth. There are also modifications of the AM muscle. 1) Section A1α has a broad insertion over the anterolateral face of the maxillary blade, 2) in some taxa there is a partial to complete separation of the A1α into two sections (*Prionurus* + *Paracanthurus* + *Zebrasoma* + *Acanthurus* + *Ctenochaetus*), and 3) these two sections (A1α′ and A1α″) become well separated anteriorly with distinct attachment sites on the maxilla (*Acanthurus* + *Ctenochaetus*) (67). Overall, within Acanthuridae, these changes to the jaw and the AM complex appear to enhance dexterity of the upper jaw by resulting in multiple points of A1 attachment on the maxilla, providing multiple points of control, and the potential for complex motions.

Furthermore, based on previous myological work and detailed dissections for a total of 87 species, we found a major difference between the Zanclidae + Acanthuridae clade, and other closely related lineages (*SI Appendix*, Fig. S6). For Zanclidae + Acanthuridae, we found that the A1 adductor muscle, which attaches onto the maxilla, and therefore is most likely the muscle generating lateral jaw rotation, attaches fully on the lateral face of the maxilla. For the vast majority of other closely related lineages, this muscle inserts onto the medial face of the maxilla. We do note the presence of a minor muscle component (A1α) attaching on the lateral face of the maxilla within the Pomacanthidae and two species of Chaetodontidae (*C.trifasciatus* and *C.meyeri*); however, we did not detect any lateral motion in these lineages when species within these families were filmed from the anterior view. Furthermore, previous work has associated the function of this morphology with jaw retraction (23). In essence, these results suggest that the attachment of the A1 AM subsection(s) on the lateral face of the maxilla, as opposed to the medial, may provide a more efficient lever arm for lateral jaw rotation.

To investigate the detailed kinematics of how lateral jaw functions within surgeonfishes, we landmarked 5 bites from anterior view videos of *Acanthurus chirurgus*. The maximum lateral jaw angle recorded in the videos was 31.2° away from the midline, suggesting a full range of motion of 62.4°. We also measured the same angle on three *A. chirurgus* specimens and found a mean maximum range of motion of 57.7° (±10.7 SE). When looking at the diversity of lateral jaw motions produced in either left or right direction from the midline by *A. chirurgus* when compared to a species without lateral jaw motion (*Siganus magnificus*) (Fig. 4*E*) we see a substantially higher degree of jaw motions occurring (e.g., Fig. 4*E*). Furthermore, when investigating the initiation of lateral jaw rotation relative to the headflick, we found that, on average, lateral jaw rotation is initiated at about 15.5 ms (± 4.3 SE) prior to the headflick, when a headflick occurs (*SI Appendix*, Fig. S4). Both of these results strengthen our hypothesis that lateral jaw rotation is a primary component of algal detachment and that it allows a higher degree of jaw dexterity.

Some species of surgeonfishes did not use lateral jaw rotation during initial algae detachment, but instead, used it postdetachment, while processing algae held within the jaws (e.g., *A. nigrofuscus*). For a view on the frequency of use of lateral jaw rotation specifically during detachment for surgeonfishes, see *SI Appendix*, Fig. S5. Our results also point to a functional interpretation to the complex nature of surgeonfish teeth and other lineages with multicuspid teeth (e.g., refs. 70, 71). By gripping algae in the jaws and moving the jaws laterally, the algae is exposed to the cutting surfaces of these teeth. Our videos and the species morphology suggest that lateral motion of the upper jaw is used to shear and cut the algae that becomes trapped between the many cusps on the teeth. There appears to be a tradeoff between the anteroposteriorly elongated jaws of *Zanclus* which increase the range of lateral motions and the shorter jaws of surgeonfishes, that appear to convey controlled lateral forces for cutting algae against the complex surfaces of the teeth.

Materials and Methods

Anatomy. To gain an understanding of the morphological features of the feeding apparatus, we used micro-CT scanning. A single *Z. cornutus* individual of 80 mm Standard Length (SL) fixed in formalin and stored in 70% ethanol was dissected under a stereoscope. The head was scanned with a MicroXCT-200 CT specimen scanner (Carl Zeiss X-ray Microscopy Inc., Pleasanton at the Center for Molecular and Genomic Imaging (CMGI), University of California, Davis. During the scanning, the specimen was kept in 70/30% ethanol/water solution to prevent tissue dehydration. Imaging was done using a beam power of 40 kV/8 W, with no filter. The voxel resolution was 13.85 μm. All projections were used for image reconstruction and a smoothing filter of 0.6 kernel size was applied to decrease image noise. Reconstruction was done using Zeiss XM Reconstructor software to produce a TXM file. The TXM file was then exported as a 16-bit raw tiff containing all projections and imported to Dragonfly ORS where segmentation was performed, and each bone was visualized using a smooth mesh.

Feeding Observations. Feeding observations for all species were conducted in the lab in accordance with the University of California, Davis Institutional Animal Care and Use Committee, protocol numbers 22,206 and 23,818. Individuals were filmed using a Photron Fastcam Mini camera fitted with a Nikon AF Nikkor 50 mm f/1.8D lens. Fish were kept and filmed in 200 l aquaria with an external canister filter on each aquarium, at a room temperature of about 25 °C. Individuals were filmed feeding on prey (e.g., algae, prawn pieces, agar plates) attached to the benthos. All individuals were acquired from commercial vendors. Individuals were initially acclimated for approximately a week prior to filming. Once individuals were acclimated and were observed to feed regularly, filming with food treatments was initiated. On nonfilming days, individuals were given a mix of algae pellets and/or frozen foods. The camera was set up in front of and perpendicular to the aquarium, along with a flood light facing the aquarium at an approximately 45° angle. Two sets of feeding trials were conducted: One set recorded the frontal view, whereas another set recorded the lateral view. Between 5 to 10 sequences per individual were recorded for each viewing angle (except for *Ctenochaetus* that did not detach algae, resulting in all bites being in the lateral view), resulting in a maximum of 20 sequences for each individual. Recordings were made at 1,000 frames per second. Each filming session lasted about 2 h, or when fish stopped feeding. A total of 674 videos were analyzed from 68 individuals across 35 species, with 1 to 4 individuals being filmed for each species. For a detailed breakdown of the species filmed, the sample size of videos for each species, and the size range for each species, see *SI Appendix*, Table S3.

Bite Rate Meta-Analysis. A meta-analysis on bite rates was conducted by searching through publications on lineages that utilize biting (i.e., detachment of attached material) as their primary feeding mode. To minimize bias that may influence bite rates due to temperature, only families from tropical reef-associated fish were included in the search. Data were procured either from direct description in the text or from published plots using WebPlot Digitiser. If only a single report of a bite rate was found for a family, this family was not used for further analysis. We also recorded the method of bite rate quantification. While most studies quantified rates through timed counts while following fish using snorkel or SCUBA, some studies used camera deployments and thus filmed only within a specific location. To keep the methodology consistent, we only used data from studies using snorkel and/or SCUBA, where an observer follows a fish for a certain amount of time (typically 10 to 15 min). Species were subsequently grouped into families. Given our results, we also removed any data for *Ctenochaetus* species, *A. leucosternon*, and *A. japonicus* which were not found to conduct lateral jaw motions.

Data Analysis. Videos for which kinematic variables were extracted were exported to the software ImageJ, where different sets of landmarks were placed on the transverse and lateral videos. For feeding sequences filmed in the frontal view, three landmarks were placed throughout the sequence. The first two were placed along the midline of the neurocranium, whereas the third was placed on the anterior-most tip of the upper jaw (Fig. 3). This set of landmarks allowed us to capture the lateral rotation of the jaw relative to the rest of the head, as well as calculating the velocity of movement of the tip of the jaws during lateral head flicks. For feeding trials recorded in the lateral view, we placed seven landmarks (Fig. 3). For a detailed description of the landmarks, see *SI Appendix*, Table S2. All landmarks were placed every five frames (5 ms) throughout the entirety of the bite sequence. Kinematic landmark data were then exported to the R software (72) for further analysis.

Once imported into R, kinematic profiles were generated for each bite sequence. This was done by calculating specific angle changes throughout the sequence using sets of three landmarks. Based on the kinematic profiles produced for specific motions, we calculated the onset, duration, and ending of the key motions found in the videos. For angles calculated from videos in the lateral plane, we used the law of cosines to calculate the angle between three points (i.e., landmarks):

$$\theta_1 = cos^{-1}\left(\frac{a^2+b^2-c^2}{2ab}\right),$$

where *a*, *b*, and *c* represent the sides of a triangle formed by the three landmarks. To account for the bidirectionality of the jaw rotation for videos in the transverse plane, we used the *atan2* function in the software R which converts rectangular coordinates to polar. This allowed us to quantify the directionality of jaw rotation relative to the rest of the head, as well as the direction of the subsequent sideways head-flick. Velocity was calculated based on the distance landmarks had moved along both x and y-axes between timesteps (i.e., 5 ms), using the following function:

$$v = \sqrt{(x_t - x_{t-1})^2 + (y_t - y_{t-1})^2},$$

where x_t and y_t represent the x and y coordinates of a landmark at a given time (t). Plots were produced using the *ggplot2* R package (73).

Statistical modeling for the bite rate metanalysis was conducted using Generalized Linear Models (GLM) following (74), where standardized bite rate (per minute) were the dependent variable, and fish families were the independent variable. A model with a Gaussian distribution was compared to a model with a Gamma distribution, and the two models were compared using the Akaike Information Criterion (AIC). Model validation (e.g., residual plots, homogeneity of variance) was done using the *performance* R package (75).

Phylogenetic Analysis. We scored each filmed fish on whether or not they utilized lateral jaw movement during resource detachment and scored whether the trait was present or absent in a species. We then reconstructed the history of this trait on a phylogenetic tree to assess its distribution across surgeonfishes and other lineages of benthic-feeding reef fishes. The phylogenetic tree used for our study was sourced from (76) and was pruned to include only the species in our study. To assess the phylogenetic history of lateral jaw rotation (presence/absence), we carried out an ancestral reconstruction using stochastic character mapping (*simmap*) in the *phytools* R package (77). We simulated 100 stochastic maps with Markov Chain Monte Carlo (mcmc) sampling and a sampling frequency of 1. The posterior probability density of each state on our phylogenetic tree was then summarized using the *density Map* function.

Data, Materials, and Software Availability. Kinematic and metanalysis data have been deposited as Excel files in figshare (https://figshare.com/account/home#/projects/241640) (78).

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