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SYMPOSIUM

The Teleost Intramandibular Joint: A mechanism That Allows Fish to Obtain Prey Unavailable to Suction Feeders

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Synopsis Although the majority of teleost fishes possess a fused lower jaw (or mandible), some lineages have acquired a secondary joint in the lower jaw, termed the intramandibular joint (IMJ). The IMJ is a new module that formed within the already exceptionally complex teleost head, and disarticulation of two bony elements of the mandible potentially creates a “double-jointed” jaw. The apparent independent acquisition of this new functional module in divergent lineages raises a suite of questions. (1) How many teleostean lineages contain IMJ-bearing species? (2) Does the IMJ serve the same purpose in all teleosts? (3) Is the IMJ associated with altered feeding kinematics? (4) Do IMJ-bearing fishes experience trade-offs in other aspects of feeding performance? (5) Is the IMJ used to procure prey that are otherwise unavailable? The IMJ is probably under-reported, but has been documented in at least 10 lineages within the Teleostei. Across diverse IMJ-bearing lineages, this secondary joint in the lower jaw serves a variety of functions, including: generating dynamic out-levers that allow fish to apply additional force to a food item during jaw closing; allowing fish to “pick” individual prey items with pincer-like jaws; and facilitating contact with the substrate by altering the size and orientation of the gape. There are no consistent changes in feeding kinematics in IMJ-bearing species relative to their sister taxa; however, some IMJ-bearing taxa produce very slow movements during the capture of food, which may compromise their ability to move prey into the mouth via suction. Despite diversity in behavior, all IMJ-bearing lineages have the ability to remove foods that are physically attached to the substrate or to bite off pieces from sessile organisms. Because such prey cannot be drawn into the mouth by suction, the IMJ provides a new mechanism that enables fish to obtain food that otherwise would be unavailable.

Background

The teleost skull is composed of more than 100 bones that constitute multiple modules, or functional units, that are able to move relative to one another (Fig. 1), thereby producing both feeding and respiratory behaviors. In contrast with the vast majority of extant tetrapods, derived teleost fishes have retained, and even expanded, the number of joints present in the cranium (Liem et al. 2001). Because of this, the teleost cranium is often considered to provide an evolutionary “tool kit” that allows multiple functional modules to evolve independently of one another (e.g., Hulsey et al. 2005). Indeed, the complex of bones that comprise the teleost neurocranium and jaws often is cited as a primary reason for the evolutionary success of this group of vertebrates (Lauder 1982).

Within the complex anatomy of the neurocranium and jaws, one module has been the focus of the majority of functional studies of feeding behaviors: the anterior jaws complex. The majority of teleost species possess a lower jaw that is formed by three bones (dentary, angular, and articular) that fuse during development into a single bony element, termed the mandible. This bony element is linked to the neurocranium via three other complexes the suspensorium, the opercular series, and the hyoid series (Fig. 1). In most teleosts, the jaw opens when input from the

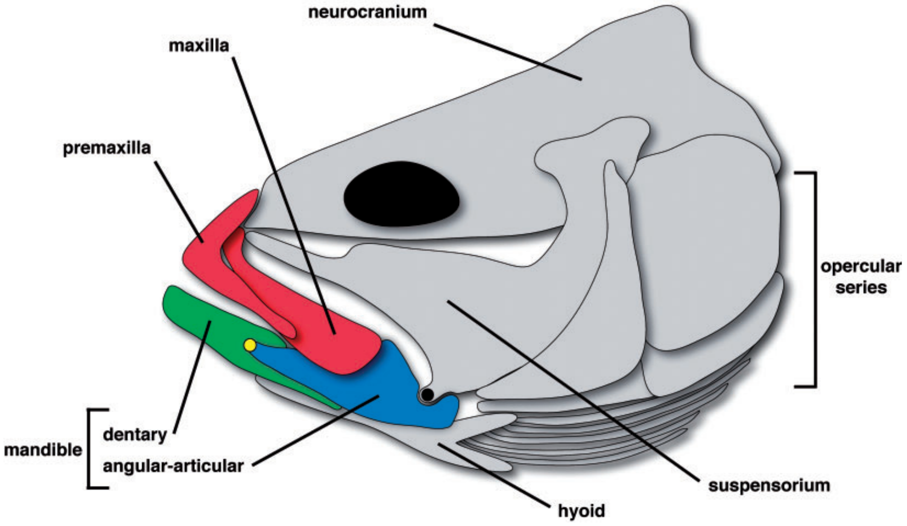

Fig. 1 The teleost skull is composed of a large number of (100+) bones that form a series of functional units; illustrated here is a generalized teleost skull (following Gregory 1933) that is composed of the neurocranium, the opercular series, the suspensorium, the hyoid series, and the anterior jaws. These functional units are themselves formed by complexes of bones; the suspsensorium, for example, is composed of more than seven individual bones that grow together during development. The anterior jaws are a functional unit that is composed of the upper jaw (the maxilla and, in many teleost, the premaxilla) and the lower jaw (or mandible). In the vast majority of teleosts, the mandible is formed by bones that fuse during early development: the angular-articular and the dentary (light circle). In these species, the lower jaw rotates about its articulation with the suspensorium (the quadratomandibular joint: black circle) during feeding. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

hyoid series, the opercular series, or both, compel the mandible to rotate about its articulation with the suspensorium. The resulting ventral movement of the anterior region of the mandible is often termed ‘‘lower jaw depression’’; this is the primary movement that underlies the production of mouth-opening (or gape) during feeding in most teleost fishes.

Although the majority of teleosts possess a fused lower jaw as described above, some species have acquired an additional joint termed the intramandibular (‘‘within the mandible’’) joint, or the IMJ. The IMJ facilitates intramandibular bending, or movement that occurs *between* two individual bony components of the lower jaw; during this movement, the dentary bone rotates about its articulation with the angular-articular. The disarticulation of formerly fused bony elements of the mandible (*via* unknown developmental mechanisms) creates a ‘‘double-jointed’’ jaw in the species that possess this morphology. Thus, the IMJ is a new module that has formed within the already exceptionally complex teleost head. Remarkably, an intramandibular joint appears to have evolved independently multiple times (Fig. 2)—each time creating a ‘‘secondary’’ jaw joint and disarticulating two formerly fused elements of the lower jaw (Fig. 1).

The apparent independent acquisition of this new functional module in several teleost lineages raises the following suite of questions. (1) How many teleostean lineages contain species with a documented IMJ? (2) Does the IMJ serve the same functional and/or ecological purpose in all species that possess it? (3) Is the acquisition of an IMJ associated with changes in the feeding kinematics in species that possess it? (4) Do IMJ-bearing fishes experience functional trade offs with other aspects of feeding performance? That is, is there a ‘‘cost’’ to having an IMJ? (5) Finally, do fishes that possess an IMJ capture food that can be acquired via suction feeding, or is the IMJ used in procuring prey that otherwise are unavailable?

Which teleostean lineages possess an IMJ?

It is often assumed that traits that have independently evolved multiple times possess adaptive significance. However, similar morphological traits could also be driven by key genetic regulatory networks (i.e., those that are responsible for the development of the trait) being repeatedly altered under a variety of selective pressures (Wake et al. 2011). To date, relatively few studies have considered the IMJ within a phylogenetic context (but see Konow et al. 2008; Price et al. 2010). Thus, examining the occurrence of the IMJ in light of recently hypothesized relationships among teleost fishes (*sensu* Near et al. 2012, 2013) may further our understanding of the number of times the IMJ has

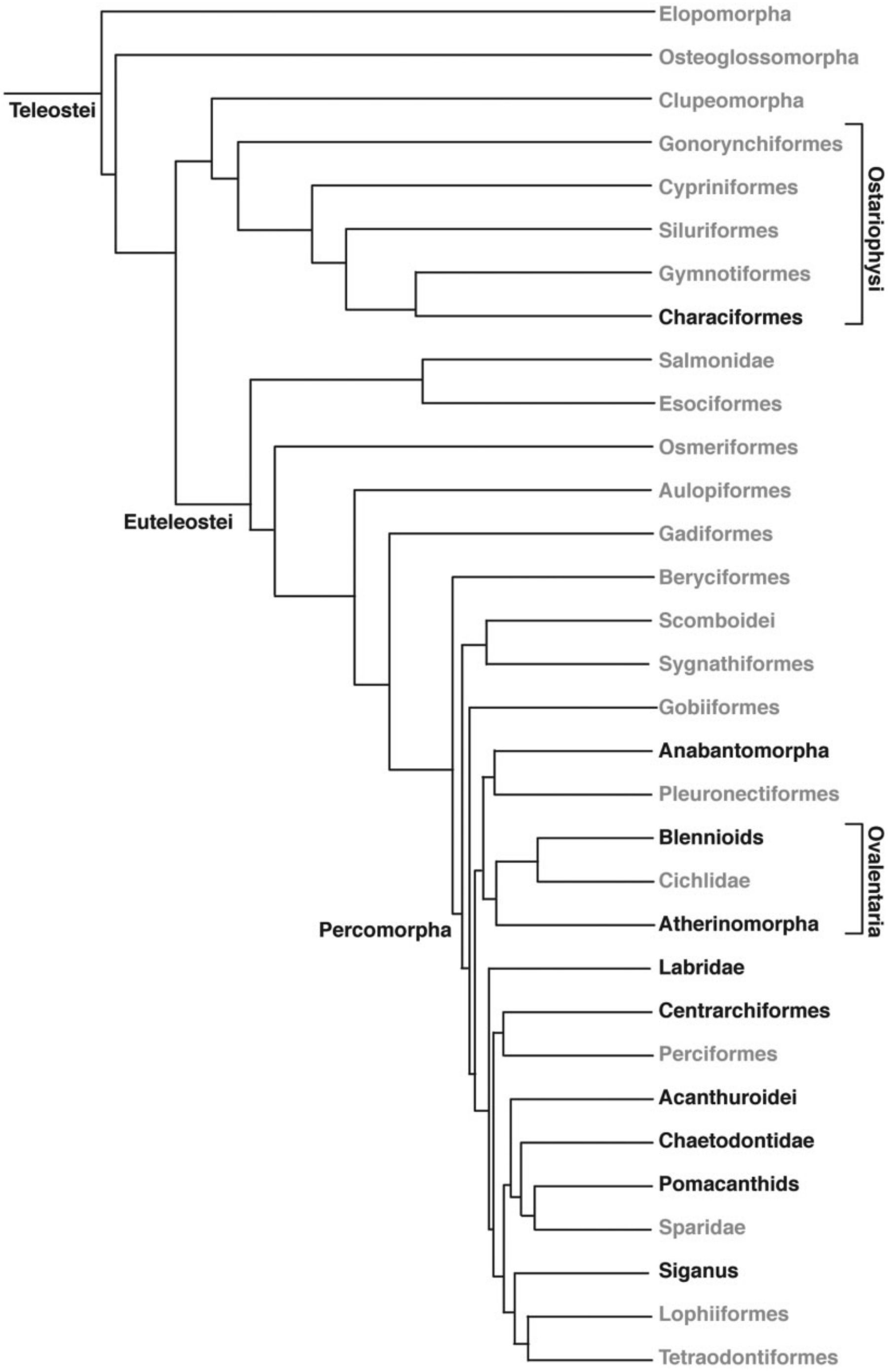

Fig. 2 The IMJ has evolved many times within the Teleostei. Hypothesized relationships among extant taxa are depicted here, with lineages that possess species with an IMJ indicated in bold. Phylogenetic relationships illustrated here are summarized from recently published molecular phyolgenies (Near et al. 2012, 2013).

evolved in the Teleostei (Fig. 2), which will provide a framework for future analyses of convergence (or divergence) in development, morphology, and ecological function.

Included here is a review of taxa for which an IMJ has been reported in the literature, although this is likely to be an underestimate of its prevalence within the teleosts because the anatomical changes can be subtle (Ferry-Graham and Konow 2010). In the past five years, several robust molecular analyses of interrelationships of actinopterygians have defined new groups (and as such, resulted in new taxonomic placements of some species); the relevant nomenclature will be given here for the lineages known to contain species that possess an IMJ. New hypotheses of interrelationships among these taxa (Near et al. 2012, 2013) may also affect the interpretation of the number of independent origins of traits of interest within the group.

The majority of documented IMJs fall within the Percomorpha, but an IMJ is present in species from at least one ostariophysan lineage (Fig. 2). Within the Ostariophysi, several characiform species possess a disarticulation between the dentary and angular-articular (Buckup 1993; Richard Vari, personal communication). However, the characiform IMJ has not yet been examined in a functional context.

The first IMJ to be described in the literature was that of the kissing gourami, *Helostoma temminckii* (Liem 1967). This genus falls within the anabantomorph clade, nested within a percomorph clade that also includes carangiforms as well as pleuronectiform flatfishes (Fig. 2) (Near et al. 2013). As such, the IMJ in kissing gouramis likely represents a single independent origin of the joint.

Ovalentaria is a newly defined clade (Wainwright et al. 2012) that comprises over 4800 species; this new clade has been corroborated by several recent studies in molecular phylogenetics (Betancur-R et al. 2013; Near et al. 2013). The diverse ovalentarian lineage is the sister group to the anabantamorph+carangiform+pleuronectiform clade (Fig. 2; Near et al. 2013). Atherinomorphs are the most basal lineage of the Ovalentaria, which also consists of cichlids, embiotocids, pomacentrids, mugilids, gobiesocids, and—the most derived lineage in the clade—the blennioids.

IMJs are present in members both of the basal and of derived lineages of the Ovalentaria (Fig. 2). Poeciliids (e.g., mollies, guppies) have a well-documented IMJ (Gibb et al. 2008) and are derived members of Atherinomorpha from the order Cyprinodontiformes. The blennid coral-reef genus *Escenius* also has an IMJ (Springer 1988, Konow and Bellwood 2005). A comprehensive molecular-systematic study of cyprinodontiforms is currently lacking (but see Parenti 1981; Ghedotti 2000; Hrbrek et al. 2007; Hertwig 2008; Costa 2012), but current knowledge suggests that Poeciliidae are a derived lineage within the Cyprinodontiformes. Thus, representatives from two independent lineages of derived ovalentarians possess an IMJ.

Parrotfishes, such as the genus *Scarus*, also have a well-documented IMJ (Tedman 1980; Bellwood 1994; Streelman et al. 2002). Previously placed within the family Scaridae, this genus now falls within Labridae (Bellwood 1994; Westneat and Alfaro 2005, Near et al. 2013), a family comprising primarily species that lack an IMJ. To date, *Scarus* is the only labrid genus known to possess an IMJ.

The herbivorous genus *Girella* also has a well-documented IMJ (Vial and Ojeda 1990, 1992; Konow et al. 2008). This genus is a member of the family Kyphosidae (Yagishita et al. 2002; Nelson 2006), which was formerly part of the catchall Perciformes but has recently been proposed as part of the sister group to perciforms, the Centrarchiformes (Fig. 2) (Near et al. 2013). Other centrarchiforms such as bluegill sunfish and largemouth bass are some of the best-studied suction feeders (e.g., Lauder 1980; Carroll et al. 2004; Day et al. 2005), but *Girella* uses a different feeding strategy with this additional joint. The kyphosids are also known as the ‘‘nibblers’’, a term that alludes to the biting or nipping mode of foraging used by many members of the family (Ferry-Graham and Konow 2010; Clinton Moran, personal observation).

Several IMJs are present within a derived percomorph lineage that includes reef-living fishes that bite their prey, such as acanthuroids, chaetodontids, pomacanthids, and sparids (Fig. 2), along with Haemulidae and 10 other families (not shown; Near et al. 2013). The most basal acanthuroid lineage within this clade includes the surgeonfishes, although the IMJ-bearing species within this group (e.g., *Acanthurus* and *Ctenochaetus*) (Purcell and Bellwood 1993) are derived within the acanthuroids (Near et al. 2013). The pomacanthid marine angelfishes and the chaetodontid butterflyfishes are nested among the other families of the clade. Some pomacanthid and chaetodontid species possess an IMJ that has been the subject of several comprehensive functional studies (Konow and Bellwood 2005, 2011) and evolutionary treatments (Konow et al. 2008). It is possible that the IMJ evolved once at the base of this clade, but given that there are almost a dozen families within this group that lack an IMJ, it is parsimonious to hypothesize three independent origins of the trait. Indeed, three independent origins of the IMJ was the conservative estimate found by Konow et al. (2008) and this was based on a tree topology that suggested closer relationships than suggested by Near et al. (2013).

Finally, *Siganus*, a genus of rabbitfishes, also possesses an IMJ (Konow et al. 2008). This genus previously was placed within the above group of reef biters (Tyler and Sorbini 1999), but is now placed in a derived percomorph clade that includes lophiiforms and tetraodondtiforms. As such, this would suggest yet another independent origin of the IMJ.

Based on what has been documented in the literature, representatives from at least 10 teleostean lineages possess an IMJ. However, this is probably an underestimate; there are likely to be many undocumented occurrences of the IMJ across such a diverse and species-rich group. It has been hypothesized that lineages have radiated and diversified following the acquisition of the IMJ (Konow et al. 2008). However, both the independent origins of the IMJ within teleosts and the patterns of adaptive radiations in IMJ-bearing lineages are as yet unclear and warrant future quantitative analysis of the evolution and diversification of this trait.

Does the IMJ serve the same functional purpose in all species that possess it?

Given the large number of functional modules that are present in the teleost skull, why have IMJ-bearing species acquired yet another functional module? Is there a particular feeding behavior or feeding mode that is associated with the presence of an IMJ? In marine taxa, the IMJ has been linked with a biting or dislodging mode of feeding (Bellwood et al. 2010; Ferry-Graham and Konow 2010; Moran and Ferry 2014). Freshwater species are less well studied from an ecological vantage point, but the presence of an IMJ appears to be associated with feeding from the substrate, at least in poeciliids (Ferry-Graham et al. 2008; Gibb et al. 2008; Hernandez et al. 2008; Hernandez et al. 2009) and in *Helostoma*, the kissing gourami (Ferry et al. 2012). Because the jaws are placed in direct contact with the food in all of these taxa, it is tempting to infer that all IMJ-bearing taxa are functionally convergent. However, it is clear that in key behavioral and mechanical aspects of the capture of prey, IMJ-bearing taxa are remarkably diverse (Fig. 3) (see also Konow et al. 2008). Four examples are given here to illustrate functional differences across IMJ-bearing taxa.

Example 1: Pomacanthus semicirculatus *(Pomacanthidae), a marine benthivore.*

In many species of teleost, the fused mandible (dentary plus angular-articular bone) rotates through a large arc about its articulation with the suspensorium complex (the quadrate-mandibular joint, or

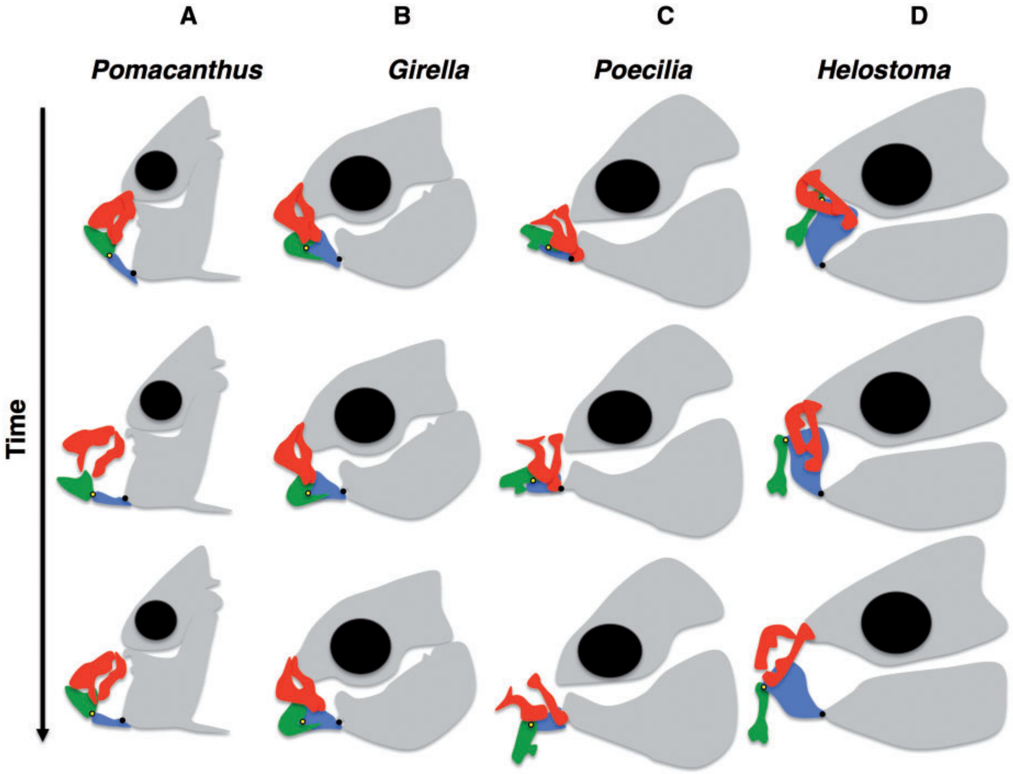

Fig. 3 Four unrelated taxa that possess an IMJ (illustrated as a light-colored circle) are characterized by distinct cranial movements during the capture of food; cranial bones are illustrated following Figure 1. (**A**) In *Pomacanthus,* the marine angelfish, the dentary bone rotates dorsally about the IMJ (toward the upper jaw) to close the mouth during food-capture as the upper jaw remains protruded. (**B**) In *Girella*, a marine chub, movement about the IMJ occurs when the lower jaw is pressed against an unyielding substrate, which causes the lower jaw to shorten. (**C**) In *Poecilia*, the freshwater, herbivorous molly, a very large rotation occurs about the IMJ; this movement allows fish to reorient their jaws toward the benthos. (**D**) In *Helostoma*, the kissing gourami, rotation at the IMJ enables fish to press the anterior jaws against the substrate when scraping off attached food. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

QMJ) to close the jaws during the capture of prey. In addition to rotation at the QMJ, angelfish (*Pomacanthus semicirculatus)* can produce rotation about the IMJ that swings the dentary bone dorsally (Fig. 3A) to close the mouth with the upper jaw elements protruded (Konow and Bellwood 2005). In this scenario, the IMJ does not appear to expand the gape in any way, which is in contrast with many other IMJ-bearing taxa (e.g., Example 4). Rather, this IMJ allows angelfish to effectively procure sessile prey, such as sponges, using a grab-and-tear method. Further, while not considered extensively by Konow and co-authors, this particular configuration of the IMJ should yield a more forceful bite due to the shortening of the lower jaw (see Example 2).

Example 2: Girella laevifrons *(Kyphosidae), a marine herbivore.*

During capture of prey, the lower jaw (mandible) of many teleost species functions as a simple third-order lever that produces bite force (Westneat 2003). Passive movement occurs at the IMJ during feeding in the marine chubs, *Girella laevifrons* and *Girella nigricans,* (Fig. 3B), as the jaws come into contact with the substrate. When this happens, rotation about the IMJ causes the lower jaw out-lever to shorten (Ferry-Graham and Konow 2010). This shortened out-lever should increase the production of force at the tips of the dentary, even in the absence of changes to the muscles that power the lever system (Ferry-Graham and Konow 2010). Interestingly, the IMJ might rightly be considered a ‘‘cheat’’ to the force-velocity trade off, as engineering-derived four-bar linkage models predict that velocity is amplified during opening of the jaw, whereas lever-based mechanical models predict that closing of the jaw is highly force-modified by the presence of the IMJ. Increased production of force at the tip of the dentary allows these specialists to remove diatoms and encrusting algae, thought to be an underutilized food resource in the marine realm (Moran and Ferry 2014).

Example 3: Poecilia sphenops *(Poeciliidae), a freshwater herbivore.*

Many species within the Poeciliidae produce bending at the IMJ joint, although the magnitude of rotation at this joint varies across taxa (Gibb et al. 2008). The best-studied species within this clade is *Poecilia sphenops*, the common black molly, a primarily herbivorous freshwater fish (Fig. 3C). In the black molly (and in its sister taxon *Poecilia mexicana*, the short fin molly), the very large amount of bending (>90°) that occurs at the IMJ appears to enhance several aspects of feeding (Gibb et al. 2008). (1) A very large total gape is produced (with ∼180° gape angle), relative to non-IMJ bearing sister taxa. (2) The upper and lower jaws can be placed in direct contact with the substrate to remove prey by scraping or pinching off pieces of food. (3) The jaws can be rotated ventrally to remove food from the benthos (Fig. 3C), whereas the body maintains a horizontal posture in the water column; this may enable a feeding fish to more readily detect and evade predators during bouts of feeding.

Example 4: Helostoma temminckii *(Helostomidae), a freshwater herbivore.*

In *Helostoma temminckii*, the kissing gourami, the IMJ appears to aid (Fig. 3D) in the production of a very large, circular opening to the mouth, with 360° of contact with the substrate (Ferry et al. 2012). Thus, all portions of the mouth-opening come into contact with the substrate during a scraping or biting motion. The 360° contact should also increase the residence time of the teeth on the substrate as the jaws are drawn together during closing of the mouth. In contrast to the force-modification role of the IMJ described above for the marine chubs, *Girella sp.*, the IMJ of *Helostoma temminckii* may be best categorized as an adaptation that modifies jaw amplitude. This could be advantageous when scraping microalgae and diatoms, which are the major components of the diet of *H. temminckii* in the wild (Asyari 2007).

From these examples, it is clear that the independent acquisition of the IMJ in many teleost taxa is not, in the strictest sense, functional convergence. Rather, diversity in anatomy, mechanics, function, and ecology suggests that this joint may serve a different purpose (or suite of purposes) in the taxa that have acquired it. Yet, in each instance, IMJ-bearing individuals use their jaws to procure sessile or attached food.

Is the acquisition of an IMJ associated with changes in feeding kinematics?

Suction feeding is thought to impose hydrodynamic constraints on the movements of the neurocranimum of teleost fishes during the capture of prey. Specifically, a wave of anterior-to-posterior expansion is retained across diverse clades that are separated by millions of years of evolution (e.g., Gibb and Ferry-Graham 2005). In addition, recent work suggests that mid-water ram feeders and biters may have fundamental aspects of their feeding behaviors influenced, or constrained, by interactions with the fluid that surrounds them (e.g., Ferry et al. 2015). All IMJ-bearing taxa studied to date feed on attached prey and experience movement at a new functional module, which is anterior to the primary (used here to mean original) jaw joint (the QMJ). Because the mechanical demands of the environment often generate convergent features in fishes that capture food via similar mechanisms (e.g., suction, ram), it is likely that IMJ-bearing taxa that consume attached prey also share key features of feeding kinematics.

To test the hypothesis that IMJ-bearing taxa are more functionally similar to one another than to size-matched, non-IMJ-bearing sister taxa, kinematic variables (Fig. 4) were collected from events recorded using high-speed imaging for six species from three clades feeding on unattached, non-elusive food. For the Poeciliidae, IMJ-bearing *Poecilia mexicana* ($n=4$) were compared with the non-IMJ-bearing *Gambusia affinis* ($n=4$). For the Anabantoidei, IMJ-bearing *Helostoma temminckii* ($n=3$) were compared with non-IMJ-bearing *Trichopodus trichopterus* (formerly *Trichogaster trichopterus;* $n=4$). For the Kyphosidae, IMJ-bearing *Girella nigricans* ($n=5$) were compared with non-IMJ-bearing *Medialuna californiensis* ($n=5$). From these videos, eight kinematic variables were measured and used in a Principal Components Analysis (PCA) (Table 1; Fig. 4) that quantified relationships among the variables. PCA is the best way to analyze these kinematic data because this method enables many non-independent variables to be summarized into a few (here, two) compound variables. The first PC, Factor 1, described more than 50% of the variance in the dataset and was weighted by five variables: four variables associated with the timing of cranial movements and one variable quantifying the degree of rotation occurring at the primary jaw joint (the QMJ). Loadings on Factor 1 did not appear to be influenced by fish size, as small individuals possessed both high and low scores for Factor 1. The second PC, Factor 2, described 25% of the variance, but this factor was heavily influenced by fish size; fish with larger bodies had higher loadings for two displacement variables (maximum gape and maximum upper-jaw protrusion). Because it appeared to be driven by body size, Factor 2 was not used to test the hypothesis that IMJ-bearing taxa are distinct from non-IMJ-bearing taxa. Scores for Factor 1, however, were used in a one-way analysis of variance (df 1, 5) and Tukey's *post-hoc* tests (conducted using SPSS 22) to ascertain whether the six species differed for this compound variable.

When each IMJ-bearing species is compared with its sister taxon, there is no consistent change across all groups in kinematics associated with the acquisition of an IMJ. For anabantoids and poeciliids, the IMJ-bearing taxa are slower and experience reduced rotation at the primary jaw joint (the QMJ) during the capture of prey, relative to non-IMJ-bearing sister taxa. In contrast, there are no statistically significant differences in timing or rotation at the QMJ when the IMJ-bearing *Girella* is compared with its close relative *Medialuna.* It appears that the diversity of behaviors and morphologies present in IMJ-bearing taxa is associated with the diversity in the cranial movements produced during the capture of food. However, it is interesting to note that two of the three IMJ-bearing taxa considered in this comparison took longer to produce jaw-opening and jaw-closing movements than their non-IMJ-bearing relatives.

Do IMJ-bearing fishes experience functional trade-offs in feeding performance?

For at least two IMJ-bearing taxa, the movements of the neurocranium and jaws during the capture of prey are slow, relative to those of non-IMJ-bearing sister taxa (Fig. 4). Producing slow movements of the head and jaws when capturing food is likely to reduce the ability to produce effective suction, especially when animals are capturing prey in the water column. Indeed, kissing gourami have difficulty procuring food from the water column and appear to only be able to suction feed when food items are floating on the surface or resting on the bottom (Ferry et al. 2012). This reduced ability to suction feed can be quantified by presenting fish with a consistent prey-stimulus (non-elusive, free-floating prey) and comparing the gape-size produced during prey capture with the distance over which the prey are displaced *via* suction. This is a useful metric of feeding performance because effective suction feeders produce small gapes that move prey over proportionally large distances (Day et al. 2005).

Within the anabantoids, individuals of *Helostoma* have a reduced ability to move prey through the water column during food capture (Ferry et al. 2012; Fig. 5). When feeding events are similarly quantified for cyprinodontiform fishes (e.g., killifishes, pupfishes, and poeciliids) feeding on non-elusive, free-floating prey, it appears that IMJ-bearing cyprinodontiform fishes also have a reduced ability to move prey through the water column and into the buccal cavity by suction when compared with their non-IMJ-bearing relatives (Fig. 5). Interestingly, *Xiphophorus helleri*, a cyprindontiform species that produces bending at the IMJ, is still able to produce effective suction when feeding on prey in the water

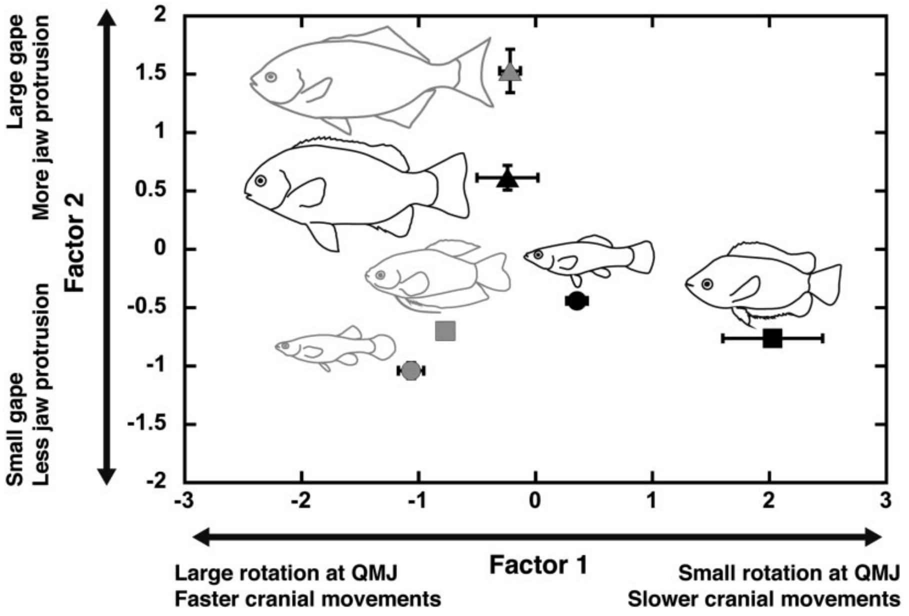

Fig. 4 PCA of eight kinematic variables measured from high-speed digital movies (120–250 fps) recorded for species representing three different teleost lineages feeding in the water column. PCA of these variables generates two compound variables that together describe more than 75% of the variance in the data (Table 1). From the Poeciliidae, IMJ-bearing *Poecilia mexicana* (black circle, $n=4$) were compared with the non-IMJ-bearing *Gambusia affinis* (gray circle, $n=4$). For the Anabantoidei, IMJ-bearing *Helostoma temminckii* (black square, $n=3$) were compared with non-IMJ-bearing *Trichopodus trichopterus* (gray circle; $n=4$). For the Kyphosidae, IMJ-bearing *Girella nigricans* (black triangle, $n=5$) were compared with non-IMJ-bearing *Medialuna californiensis* (gray triangle; $n=5$). Kinematic variables and PCA-factor weightings are as described in Table 1. Species' means (±SE) are illustrated here for PCA Factor 1 (51% of variance) versus PCA Factor 2 (25% of variance); relative size of the individuals representing each species is indicated by the size of the species' icon. Factor 2 (*Y*-axis) is weighted by maximum gape and displacement of the upper jaw while capturing food; however, this factor appears to be strongly influenced by fish size, with larger species receiving higher scores for Factor 2. Factor 1 (*X*-axis) is weighted by the timing of movements of the jaw during the capture of food and by the degree of rotation at the QMJ (Table 1). One-way analysis of variance, considering Factor 1 as the dependent variable, revealed that there are differences among the six taxa (df 1,5, $F=69.8$, $P<0.001$). For poeciliids and anabantids, the individuals of the IMJ-bearing species have significantly greater scores for Factor 1, relative to their non-IMJ-bearing relative (Tukey's HSD *post-hoc*, $P<0.005$). However, IMJ-bearing and non-IMJ-bearing kyphosids are not different from one another (Tukey's HSD *post-hoc*, $P=0.7$).

column. Individuals of *Xiphophorus* appear to be able to modulate cranial movements during feeding, such that prey positioned on the bottom are captured with slow movements of the jaws, whereas prey in the water column are procured via rapid movements of the jaw (Mackay et al. 2014).

Is the IMJ used to procure prey that are unavailable to suction feeders?

The role of the IMJ during the capture of food raises an ecomorphological question that has received relatively little attention in the past: what types of prey *cannot* be captured by suction feeding? Prey can be characterized in a number of ways, but two fundamental properties of a prey item likely determine how it can be procured: its linear dimensions (size) and its ability to move away from the predator to evade being eaten (velocity). Within this context, these two parameters can be used to map out a "prey space" that is occupied by food items that pose fundamentally different challenges for teleost fishes. Some prey are very small and move little, but may be difficult to parse out from the substrate or the water column (Fig. 6, lower left); others are large and unmoving, or physically attached to the environment (Fig. 6, upper left). Very large animals may be difficult to consume because of their size and/or because they swim at high velocities (Fig. 6, upper right); smaller prey may fit between a predatory fish's jaws, but may be extremely difficult to capture because they swim at high velocities (Fig. 6, lower right). Different prey fall into different regions of this prey space, with large, sessile organisms (e.g., corals) exemplifying one extreme, and rapidly moving, constantly swimming organisms (nekton, such as smaller fishes or squids) another. From a fluid dynamics perspective, the suction component of capture requires that a fish be in close proximity to the prey when the expansion of the

Table 1 Component matrix generated by PCA of eight kinematic variables measured from individuals ($n = 3$–5) representing six species feeding on non-elusive prey (recorded at 120–250 fps).

Kinematic Variable[a]	Factor 1 (51%)	Factor 2 (25%)
Gape distance (cm): maximum distance between upper and lower jaws	−0.10	+**0.97**
Upper jaw protrusion (cm): net distance moved by upper jaw away from cranium	−0.09	+**0.94**
Lower jaw rotation (°): change in orientation of the lower jaw, relative to the cranium	−**0.60**	−0.44
Cranial rotation (°): change in orientation of the cranium, relative to the axial body	+0.40	+0.09
Time to maximum gape (s): time from onset of rapid opening of the mouth until maximum gape occurred	+**0.94**	+0.01
Time to maximum upper-jaw protrusion (s): time from onset of rapid opening of the mouth until the maximum protrusion of the upper jaw occurred	+**0.97**	−0.04
Time to maximum lower-jaw rotation (s): time from onset of rapid opening of the mouth until maximum ventral rotation of the lower jaw occurred	+**0.95**	−0.05
Time to maximum cranial rotation (s): time from onset of rapid opening of the mouth until the maximum dorsal rotation of the neurocranium occurred	+**0.93**	−0.06

Note: Factors 1 (51%) and 2 (25%) together accounted for more than 75% of the variance in the data. Component loadings (unrotated values) are given here; components that loaded at >0.6 or <-0.6 are indicated in bold. See Figure 4 for additional details.

[a] Variables associated with hyoid movements were not quantified because they could not be measured in all individuals.

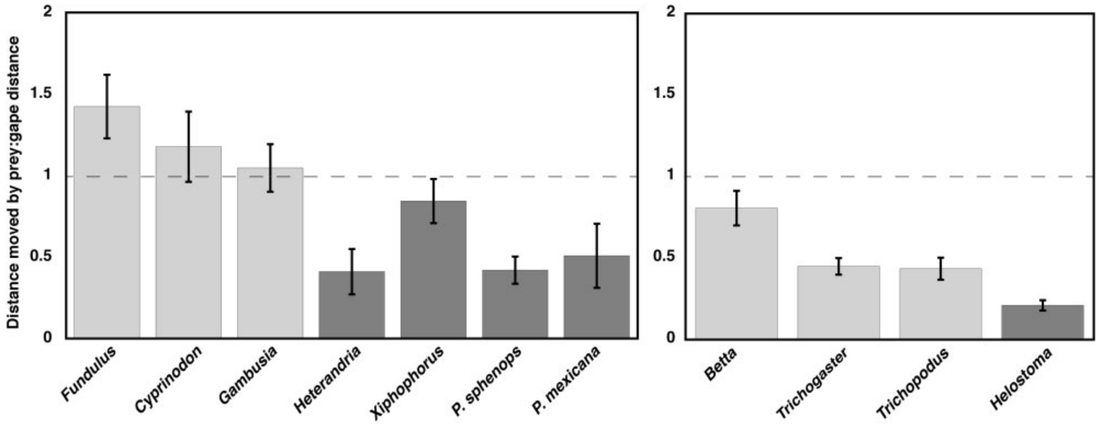

Fig. 5 For both cyprinodontiform (left panel) and anabantid fish (right panel), individuals from species that possess an IMJ (shown in dark gray) have a reduced ability to move prey into the buccal cavity from the water column, relative to non-IMJ-bearing sister taxa (light gray). Illustrated here is the ratio of the distance that prey are transported through the water column into the buccal cavity, relative to the linear distance between the tips of the upper and lower jaws (i.e., gape) produced during the feeding event; events in which the prey are moved the same distance as the size of the gape have a value of one (dashed line). Fish were provided with non-elusive prey and sequences of feeding were recorded 250 fps with high-speed digital-imaging; shown here are mean values ± 1 SE of the mean. Cyprinodontiform species included are *Fundulus rubrifrons* ($n = 8$), *Cyprinodon macularius* ($n = 8$), *Gambusia affinis* ($n = 14$), *Heterandria formosa* ($n = 18$), *Xiphophorus helleri* ($n = 11$), *Poecilia sphenops* ($n = 7$), and *Poecilia mexicana* ($n = 5$). Anabantid species included are *Betta splendens* (all were females, $n = 17$), *Trichogaster lalius* ($n = 23$), *Trichopodus trichopterus* ($n = 22$), and *Helostoma temminckii* ($n = 15$). *Helostoma* feeding events were different from events for all non-IMJ bearing anabantid species ($t = 3.6$, df 75, $P < 0.001$); similarly, feeding events for IMJ-bearing *P. mexicana, P. sphenops, Heternadria and Xiphophorus* were significantly different from events for non-IMJ bearing *Fundulus, Cyprinodon,* and *Gambusia* ($t = 5.1$, df 69, $P < 0.001$).

head occurs, and that the prey can be entrained and moved into the head by a current of water (e.g., Wainwright et al. 2007); because of these constraints, only some types of prey can be drawn into the head by suction during capture. Thus, ram-feeding, filter-feeding, biting, and picking have evolved within the context of exploiting prey in regions outside of the "suction space".

Despite the diversity in underlying mechanisms, it appears that all IMJ-bearing lineages have the ability to remove food that is attached to the substrate and/or bite off pieces of large, sessile organisms (Fig. 6,

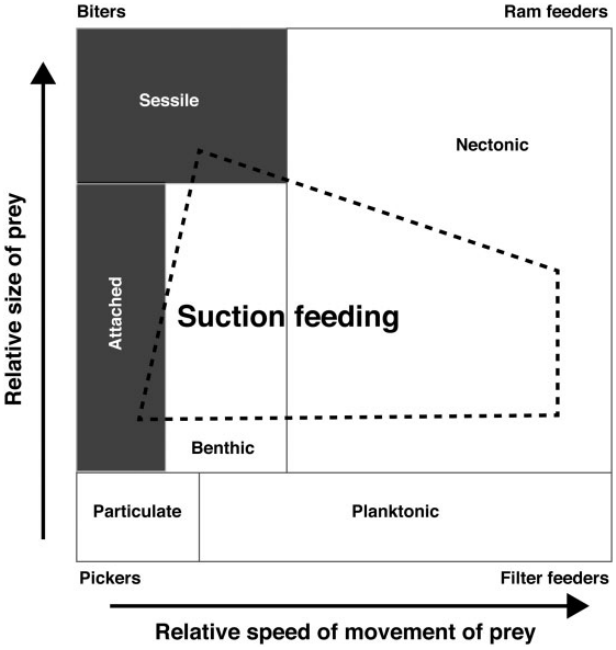

Fig. 6 Two parameters can be used to map out a "prey space" occupied by food items that pose fundamentally different challenges for teleost fishes. Some prey are small and move very little, but may be difficult to parse out from the substrate or the water column (lower left); others are large and unmoving, or physically attached to the environment with only a limited ability to move away from the predator (upper left). Suction (dashed polygon) can be used to capture freely moving benthic (bottom-dwelling) and nektonic (free-swimming) animals and may constitute a component of prey capture for other feeding modes; in many cases, however, feeding on prey outside of this "suction space" requires fish to adopt alternative mechanisms for capture. Pickers select individual, non-elusive prey that fit between the upper and lower jaws; filter-feeders trap small prey that are entrained in the water column; ram-feeders chase down elusive prey; biters shear off portions of large non-elusive prey; scrapers can apply their jaws to the substrate and dislodge attached prey. Species with an IMJ are similar to one another because they all use the anterior jaw to procure large, sessile, or firmly attached prey; this region of prey space is illustrated in dark gray in the upper and far left of the graph.

far left and upper left). Because these prey are excluded from the suction space, fishes that specialize on them have evolved new mechanisms that facilitate exploiting such resources. Non-IMJ-bearing species typically remove pieces of their food by biting, and adaptations for this feeding mode include larger jaw-closing muscles and foreshortened mandibles that enhance a fish's ability to transmit force to the prey (Alfaro et al. 2001). However, the IMJ appears to offer a suite of new evolutionary solutions to the mechanical problem of acquiring attached prey. These solutions include: dynamically changing jaw out-levers to apply additional force to a food item as required, "picking" at prey items with protruded, pincer-like jaws, increasing the gape of the mouth, and changing the orientation of the upper and lower jaws to facilitate greater contact between the jaws and attached food items.

Conclusions

Attached prey require removal by force (biting), using dexterity (picking), or *via* increased contact with the jaw (scraping). Movements of the jaws during such behaviors are typically slow, and the magnitudes of the gape are often large. These performance parameters are in opposition to movements that enhance the production of suction: small gape and rapid cranial expansion (e.g., Wainwright et al. 2007). Correspondingly, modifications of morphology and behavior that permit fish to feed on attached prey may come at a cost to their ability to capture elusive prey by suction. Comparative analyses of feeding kinematics reveal that some (although not all) IMJ-bearing species are slower than are their non-IMJ-bearing relatives, which suggests a limited ability to entrain prey in the water column via suction. A reduced ability to capture prey from the water column likely narrows the breadth of prey available to many fishes that possess an IMJ.

This raises the question: do *all* species that possess an IMJ suffer from reduced ability to feed in the water column? IMJ-bearing species are potentially double-jointed: a fish could produce rotation about the QMJ (the primary jaw joint), the IMJ (the secondary jaw joint) or both. Because there are two possible points of rotation, IMJ-bearing species may be able to "flip a switch" to produce movement at the IMJ—or choose not to use the IMJ at all, but instead rely on the QMJ. IMJ-bearing *Xiphophorus helleri* appear to use rapid movements to capture prey in the water column, and slower movements when feeding on prey attached to the bottom (Mackey et al. 2014). Similarly, *Girella sp.* may not experience movement at the IMJ when feeding in the water column, but undergo a dynamic change in the length jaw as the lower jaw is pressed against the substrate. In contrast, more specialized taxa such as *Poecilia* and *Helostoma* appear to be unable to modulate their jaw mechanics to produce effective suction when prey items are floating in the water column. For these species, the ability to exploit underutilized attached prey appears to be an ecological benefit that outweighs any loss of ability to exploit prey captured from the water column by suction.

When these and other IMJ-bearing taxa are placed within a phylogenetic context, it is clear that a secondary joint in the lower jaw has evolved many times within the Teleostei. In fact, because the anatomical changes that allow movement within the mandible can be subtle, it is likely that the IMJ is under-reported—particularly in small taxa of freshwater fish. In addition, there are likely to be different evolutionary pressures in marine versus freshwater environments because of the nature of the attached/sessile prey present in each habitat. Attached/sessile prey in the marine environment are physically larger and contain tissues that resist shearing forces during a bite (e.g., corals, coralline algae, macroalgae). The role of the demands of marine versus freshwater prey in shaping the structure and function of the IMJ across these two habitats is, as yet, unclear. Indeed, the role of IMJ in promoting adaptive radiations is similarly murky. In some cases, such as in the freshwater anabantids, the IMJ is found in one species (*Helostoma temminckii*), which is the only species in its family (Helostomatidae). In marine lineages that feed on corals, in contrast, a secondary joint in the jaw is associated with a radiation of species (Konow et al. 2008; Price et al. 2010). Much additional work remains to elucidate the role of the IMJ in generating evolutionary novelty and opening up new feeding niches in freshwater and marine environments.

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