

Unprecedented Biting Performance in Herbivorous Fish: How the Complex Biting System of Pomacentridae Circumvents Performance Trade-Offs

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ABSTRACT: It is well accepted that the complexity of functional systems may mitigate performance trade-offs. However, data supporting this theory are hard to find because they need to be based on a functional system with different complexity levels in closely related species. The Pomacentridae (damselfishes) provide an excellent opportunity to test this hypothesis because most of the species have two mouth-closing systems: the first using the *adductor mandibulae*, as in all teleost fishes, and the second relying on the ceratohyal (cmd) ligament, a synapomorphic trait of the family. Interestingly, some pomacentrids have secondarily lost the cmd ligament during evolution and therefore have a less complex mouth-closing system. Using dissection, kinematic analysis, and mathematical modeling, we demonstrated that the possession of two mouth-closing systems enabled grazing damselfishes to have a forceful and extremely fast bite. This combination challenges a major functional trade-off in fish jaw dynamics, as systems better suited for force transmission are usually less suited for speed transmission, and vice versa. The combination of grazing behavior, small and robust lower jaws (conferring high biting force), and an ultrafast bite is unusual within actinopterygians. These attributes and their associated performance seem to be required conditions to colonize the ecological niche of farming, that is, the maintenance of small filamentous algae crops serving as both food and storage.

Keywords: coral reef fishes, functional complexity, functional innovation, farming, feeding mode.

Introduction

Functional trade-offs are thought to place strong constraints on the evolution of organismal performance because the best phenotype for one task is often not the best for other tasks (Walker 2007; Holzman et al. 2011). For example, an increase in hind-limb length enhances jumping distance in *Anolis* lizards but lowers sprint speed (Bauwens et al. 1995; Toro et al. 2004). The dichotomy between transmission of force and velocity is a major morphological functional trade-off in motion (Barel 1983; Westneat 1994; Herrel et al. 2009). This trade-off is due to the nature of the lever system, a mechanism of force transfer with a stiff beam across a rotation point that may enhance either force or velocity at the end of the beam (Barel 1983). The most common type of lever mechanism found in animal jaws and limbs is a third-order lever in which the input force and the load are on the same side of the fulcrum, with the input force closer to the fulcrum than the weight (Westneat 2003). This lever mechanism can be defined by mechanical advantage (MA), that is, the ratio of the muscle moment arm (input) to the moment arm of the lower jaw (output; fig. 1A). A high value for this ratio indicates that the system is capable of high force transmission at the expense of velocity, and conversely, a low value indicates that the system is capable of transmitting high velocity at the expense of force (Gregory 1933; Barel 1983; Westneat 2003). Although lever systems alone cannot dictate the range of force and velocity achieved (e.g., Hernandez et al. 2005; Arnold et al. 2011; Maie et al. 2011; McHenry and Summers 2011), they do induce a trade-off between biting force and velocity in fish jaws (Van Wassenbergh et al. 2005; De Schepper et al. 2008). This trade-off has shaped the design of fish jaws

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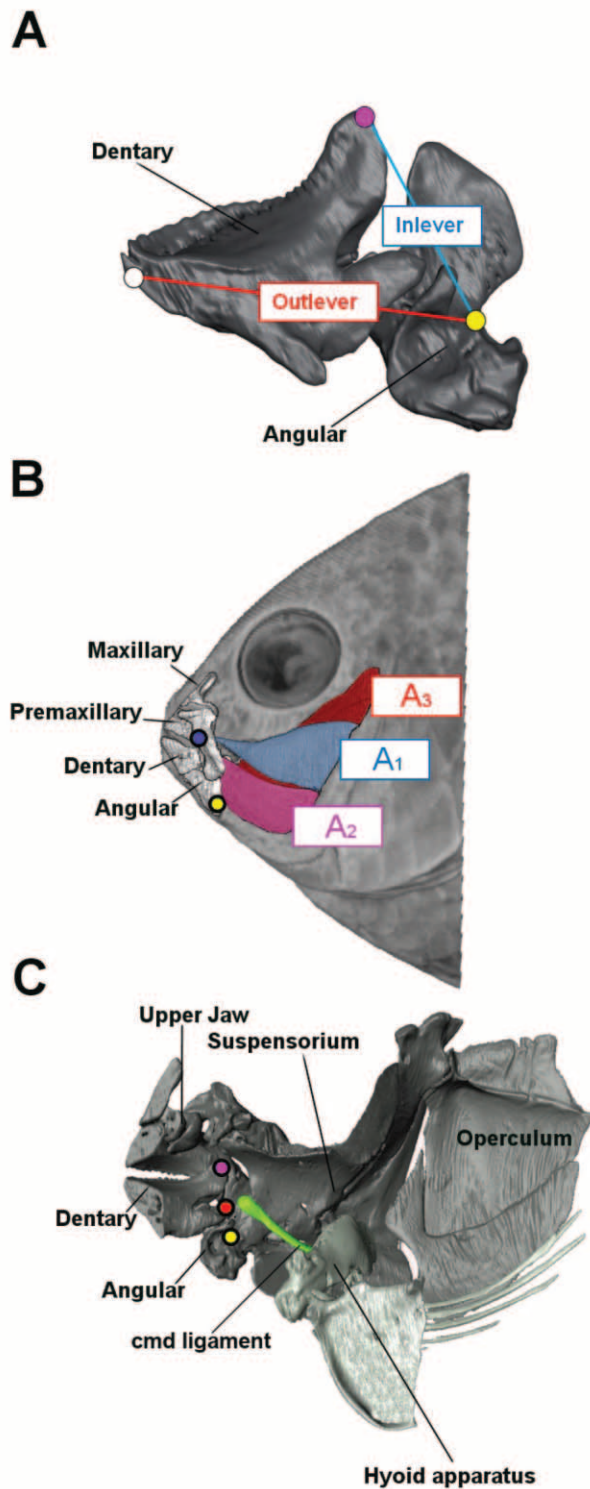


Figure 1: Morphology of the mouth-closing systems in Pomacentridae. A, The closing mechanical advantage (MA) of the A_2 bundle of the *Adductor mandibulae* (AM) on a medial view of the lower jaw of *Stegastes rectifraenum*. B, A 3-D representation of the AM in a lateral view of the cephalic region of *S. rectifraenum*. The three

related to the evolution of their feeding ecology. Manipulators that scrape, excavate, or crush their food have short and robust jaws, increasing their force-generating capacities, while fish that capture highly elusive prey (e.g., piscivores) often have elongated jaws, increasing their speed-generating performance (Richard and Wainwright 1995; Turingan et al. 1995; Wainwright and Bellwood 2002; Westneat 2004).

It is acknowledged that the functional complexity can mitigate functional trade-offs (Liem 1973; Vermeij 1973; Lauder 1982; Carroll 2001). Complex functional systems have widely been described as being determined by multiple interacting component traits (Koehl 1996; Wainwright 2007; Holzman et al. 2011). We think that functional complexity is a general concept that can be presented in various forms, each having the potential to decrease functional trade-off. This functional complexity can decouple some tasks that were previously performed by the same system or set of traits and remove constraints on the evolution of each functional component. It concerns, for example, the multiplication of the appendages in crustaceans that secondly specialized in different functions (Adamowicz et al. 2008) or the evolution of novelties, such as the pharyngeal jaws in teleosts that allow for decoupling prey capture from prey processing (Liem 1973; Hulsey 2006; Wainwright 2006). Functional complexity can also refer to a single system made up of various elements interacting together to perform one function. In that case, multiple configurations of the system underlying elements can achieve the same performance (i.e., many-to-one mapping; Wainwright et al. 2005), and the term “functional redundancy” can be used (Muñoz et al. 2017).

This functional redundancy can remove evolutionary constraints on the individual elements and may be found in many biomechanical systems, such as the four-bar linkage systems in fish and mantis shrimp (Alfaro et al. 2004; Muñoz et al. 2017), the suction feeding system in fish (Collar and Wainwright 2006), or the multiple configurations of limb-bone lengths and corresponding masses in anole lizards (Vanhooydonck et al. 2006). Functional redundancy can also occur when the addition of trait(s) create(s) distinct functional systems that shared the same function. For

main bundles (A_1 – A_3) are represented and color-coded. The yellow circle indicates the articulation around which the lower jaw rotates. The blue circle indicates the A_1 insertion on the maxillary of the upper jaw. C, A 3-D representation of the ceratohyal (cmd) ligament in a medial view of *S. rectifraenum*. Only the operculum, suspensorium, buccal jaws, and hyoid apparatus are illustrated. The cmd ligament joints the ceratohyal of the hyoid bar to the coronoid process of the angular of the lower jaw. The yellow circle indicates the lower jaw articulation, while the purple and red circles indicate the insertion point of the subdivisions A_2 and A_3 of the AMs, respectively.

example, the opening of the mouth in fishes (function) became more complex, going from a single opening system in primitive lineages to at least three different systems in derived teleosts (Lauder 1982; Huby and Parmentier 2019). The multiplication (or redundancy) of the mouth-opening systems thus allowed for a decoupling between two fundamental tasks to capture prey: the opening of the mouth and the expansion of the buccal cavity to create a suction flow leading prey to the esophagus (Lauder 1982).

Functional complexity—presented in the form of functional decoupling, structural replication, many-to-one mapping, or functional redundancy—is thought to be able to remove constraints and to mitigate functional trade-offs. However, this well-accepted statement still lacks empirical support. Indeed, direct examples of functional trade-off mitigation are hard to find because few closely related species have different levels of complexity in a functional system subject to a trade-off. For example, the trade-off between the abilities to capture attached or evasive prey in centrarchid fish can be weakened because the force that a suction-feeding fish exerts on its prey may be modified by one of three functional components: reduction in gape size, expansion of the supraoccipital crest, or increased mouth displacement (Holzman et al. 2011).

This latter example was, however, inferred from simulated variations of the level of complexity because there is no variation among species in the presence of components and therefore no interspecific difference in the level of complexity. The fish family of Pomacentridae (damselfishes) allows here an empirical test of the hypothesis that complexity mitigates trade-offs with a set of species that differ in level of complexity.

Damselfishes have two independent mouth-closing systems: biting-1 (B1), enabled by the *adductor mandibulae* (AM; fig. 1B), as observed in all teleosts (Ferry-Graham and Lauder 2001), and biting-2 (B2) provided by the ceratomandibular (cmd) ligament (fig. 1C), a synapomorphic trait joining the hyoid bar to the internal part of the mandible (Stiassny 1981). This second mouth-closing system, coupled with fast neurocranium elevation and depression of the hyoid, quickly tightens the cmd ligament, which then forces the lower jaw to close in only 2–4 ms (Parmentier et al. 2007; Olivier et al. 2014, 2015; fig. 2). This jaw-closing movement is used in at least two different tasks: sound production (Parmentier et al. 2007) and grazing filamentous algae (Olivier et al. 2014). Interestingly, the cmd ligament has been lost several times during the evolution of the Pomacentridae (Frédérich et al. 2014). The lack of this trait

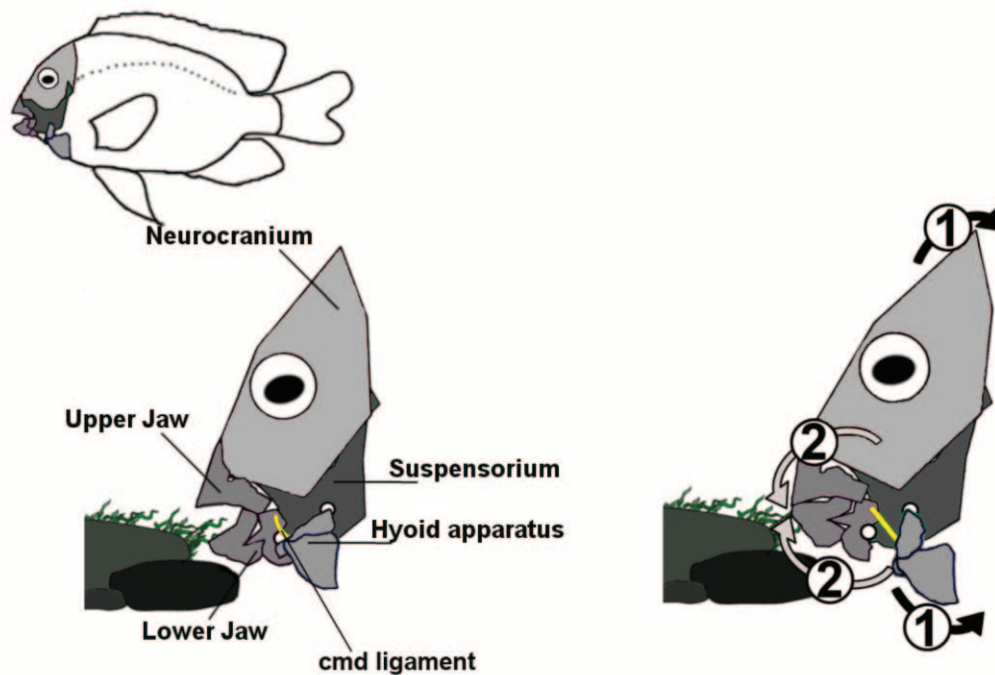


Figure 2: Biting mechanism to scrape filamentous algae in Pomacentridae. Damselfishes use an unusual biting mechanism to scrape filamentous algae. This mechanism depends on a synapomorphic trait, the ceratomandibular (cmd) ligament that joins the hyoid apparatus to the upper part of the mandible. The cmd ligament is initially loose and rapidly tightened through fast movement of the neurocranium and hyoid apparatus (1), these movements force the lower jaw to rapidly rotate around its articulation and to close in only 2–4 ms (2); see Parmentier et al. (2007) and Olivier et al. (2014) for more details on the mechanism.

is linked to (a) the absence of herbivory, all the species without the cmd ligament being zooplanktivorous (Frédérich et al. 2014), and (b) the inability to perform B2 (Olivier et al. 2016). Yet the loss of the cmd ligament removed constraints on the evolution of damselfish shapes; species lacking the cmd ligament possess elongated oral jaws and slender body forms (Frédérich et al. 2014). This distinctive shape is associated with functional specialization to a ram-feeding mode with a high amount of buccal jaw protraction to capture elusive prey (Olivier et al. 2017). The existence of closely related species with one or two mouth-closing systems (i.e., an obvious variation in the degree of complexity in the biting mechanism) facilitates the study of how functional redundancy may mitigate functional trade-offs.

Most of the grazing damselfishes are territorial, defend rich algal turfs against roving herbivores (e.g., sea urchins, parrotfishes), and harvest the algae inside their territory (Ceccarelli 2007; Hata and Ceccarelli 2016). These damselfishes are often designated as “farmers”; their territory serves as both food and storage (Hata and Ceccarelli 2016). While territorial damselfishes vary in their farming behaviors (Hata and Kato 2004), they need a sustainable extraction mode to preserve their resource. Low fecal ash content and low amounts of sediment in stomach contents from grazing damselfish suggest highly selective bites to seize algae (Wilson and Bellwood 1997; Cleveland and Montgomery 2003; Townsend and Tibbetts 2004; Ho et al. 2009; Feitosa et al. 2012). *Stegastes rectifraenum*, a farming species, approaches a patch of filamentous algae cautiously and slowly opens its mouth until the algae are surrounded by the jaws, then the fish rapidly closes its mouth using a B2 mode (Olivier et al. 2014). The mouth-closing movement is so fast that sounds related to teeth collision are clearly audible (Olivier et al. 2014). The fast bite of farmers would allow the algae to be cut accurately, decreasing deflection of the stems (see impact cutting principle; Tuck et al. 1991; Yiljep and Mohammed 2005). Although B1 and B2 are two independent mouth-closing systems, we showed that the AM and the cmd systems are used in synergy to graze filamentous algae (Olivier et al. 2014), suggesting that a forceful bite is also required. In addition to their foraging activity, the farmers also weed out undesirable algae such as macroalgae, which are more resistant than turf. They may also remove intruders such as sea urchins (Hata and Kato 2004; Irving 2019), which can represent a heavy load for these small-sized fish. Indeed, Hata and Kato (2004) showed that the sea urchin *Echinometra* species, which grows to a test diameter of ~5 cm, was automatically extruded by the ~8-cm-long *Stegastes nigricans*.

We hypothesized that the origin of the cmd ligament allowed damselfishes to circumvent the force-velocity trade-off in biting performance, which in turn enabled

the origin of farming. Accordingly, we tested four assumptions. We first assumed that the grazing damselfishes (most of them described as farming species) have an AM system configuration that provides them with a more forceful bite than nongrazers. Second, we assumed that the species without the cmd ligament have faster mouth-closing movement than species with the cmd ligament when only the AM system is considered. This increase in velocity will be due to their more elongated buccal jaws conferring them lower closing values (Frédérich et al. 2014). However, the trade-off appearing between our first and second assumptions will be circumvented by the presence of the cmd ligament, which will allow the grazing damselfishes to have a very fast bite despite their AM system configuration. Third, we assumed that in view of their combination of feeding habits, lower jaw design, and biting performance, grazing damselfishes do not follow the general evolutionary trend observed within the actinopterygians. Finally, we assumed that the innovation due to functional redundancy has been a necessary condition for the emergence of farming behavior in damselfishes.

To test our hypothesis, we compiled morphofunctional data for 29 species representing 15 genera of Pomacentridae to mathematically model the bite force and velocity with the AM system. We compared our observations to a set of kinematic data collected in previous studies (Olivier et al. 2014, 2015, 2016). Then, we compared the design of the lower jaw (MA) and the velocity biting performance of damselfishes to what is currently known in actinopterygians. Finally, we observed the co-occurrences of a forceful, ultrafast bite and farming behavior in damselfishes.

Material and Methods

All statistical analyses were performed with R software (R Development Core Team 2016). Data and the R code to run all the analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2280gb5qh>; Olivier et al. 2020).

Morphological Data and Biomechanical Model

We collected morphological data to predict the biting force and velocity produced by the AM system using a modified version of a previously published biomechanical model that calculates the angular motion of the lower jaw based on the dynamic equilibrium of the external torques acting on the system (Van Wassenbergh et al. 2005; see the appendix for further details). We dissected 82 individuals representing 29 species, 11 grazers versus 18 nongrazers, and 24 cmd species versus five noncmd

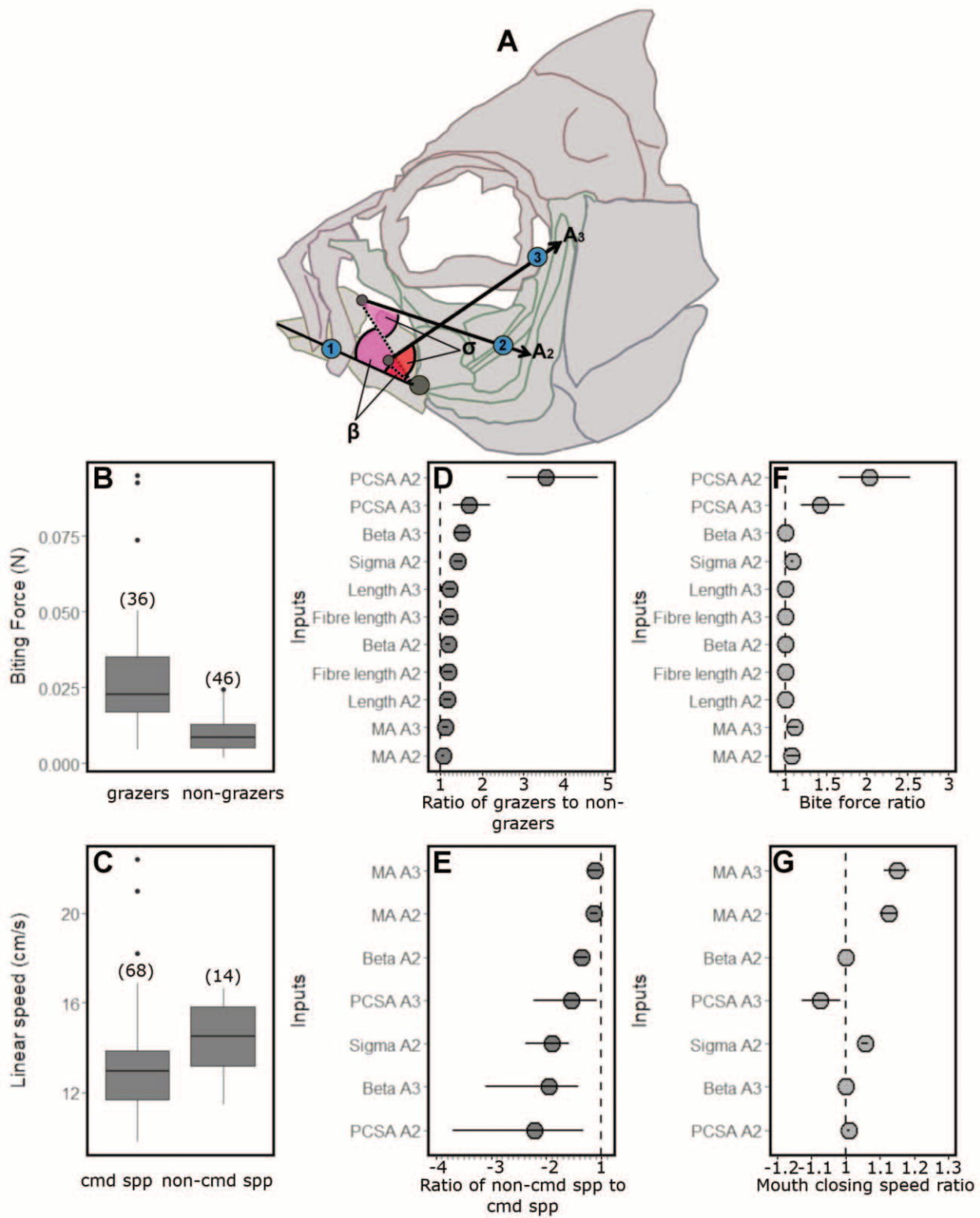


Figure 3: Bite model in the Pomacentridae. *A*, Left lateral view of a damselfish skull (*Chromis chromis*) with representation of the different variables collected for the biting model simulations. The lengths of the lower jaw and the two studied *adductor mandibulae* bundles are numerated. The in-lever is the distance between the insertion of the muscle (small gray circle) on the lower jaw and the articulation of

species (table S1; tables S1–S4 are available online). The dissected fish were a combination of specimens collected in the field (Corsica, French Polynesia, Madagascar, Mexico, Papua New Guinea, and Taiwan) and accessioned museum specimens.

Although the AM consists of three main bundles in the Pomacentridae (Gluckmann and Vandewalle 1999), our model considered only the bundles A_2 and A_3 , which directly insert on the lower jaw (fig. 3A). Our observations were made from dissection on the right side of the fish with a binocular microscope. Aided by a camera lucida, we drew several landmarks on a blank piece of paper indicating the origin of each AM subdivision, the insertion point on the oral jaws, the articulation of the lower jaw with the quadrate, and the anterior tip of the lower jaw. These landmarks were chosen based on the method developed by Westneat (2003). Measurements were made on scanned paper to the nearest 0.01 cm using the program VistaMetrix 1.36 (Skillcrest, Tucson, AZ). These landmarks allowed us to measure the following variables for each AM bundle (fig. 3A): (1) the in-lever (i.e., the distance between the insertion of the muscle on the lower jaw and the articulation of the lower jaw with the quadrate); (2) the out-lever (i.e., the lower-jaw length, measured as the distance between the articulation and the anterior tip of the lower jaw); (3) half of the width of the buccal cavity at the level of the lower jaws' articulation (based on preliminary dissections in *Chromis chromis* and *Plectroglyphidodon lacrymatus* without and with the cmd ligament, respectively, we estimated this variable as half of the lower-jaw length in species with the cmd ligament and as a third of the lower-jaw length for species lacking the cmd ligament); (4) the muscle length (the distance between the upper limit of the insertion on the suspensorium and the insertion on the mandible); (5) the muscle's tendon length; (6) the fiber length (calculated as the muscle length minus the tendon length, because we considered both muscles as not pennate to simplify the model, even though the A_3 has a small portion that is pennate [Gluckmann and Vandewalle 1999]); (7) the angle σ between the in-lever and the line of action of the muscle; and (8) the angle β between

the in-lever and the out-lever. We considered two additional variables: (9) the physiological cross-sectional area (PCSA) that was approximated by the ratio of the mass (weighed to the nearest 0.1 mg) over the fiber length (i.e., a density for muscle of 1.06 kg dm^{-3} was used); and (10) the starting mouth-opening angle (based on in vivo video recordings, we chose a start opening angle of 20°).

Comparisons of Bite Performances between Groups

To test our first assumption, we compared the bite force between the grazing damselfishes (grazers) and the others (nongrazers), as well as all the model variables. Almost all the grazers are farming species and feed mainly on the benthos (filamentous algae and benthic invertebrates). The nongrazers include the zooplanktivorous species feeding mainly on elusive prey in the water column and the omnivorous species feeding on prey in the benthic and pelagic environments in variable proportions (Frédérich et al. 2009, 2016; Gajdzik et al. 2016). To test our second assumption, we compared the bite velocity estimated by the model, as well as all the model variables between the species with the cmd ligament (cmd species) and those without this trait (noncmd species).

We first compared head length between groups and did not find any differences (estimate = 1.67, standard error [SE] = 1.01, t -value = 1.65, $P = .102$ for the grazers vs. the nongrazers; and estimate = 1.27, SE = 1.35, t -value = 0.94, $P = .349$ for the cmd vs. noncmd species). Thus, we did not perform size correction to compare the groups in the following statistical analyses.

We tested our predictions using phylogenetic-corrected ANOVAs (Garland et al. 1993) using the R function `phylANOVA.intra` (López-Fernández et al. 2014). The `phylANOVA.intra` function is a modification of the `phylANOVA` R function introduced by Revell (2012) to allow the consideration of various individuals by species. The modification is an adjustment of the evolutionary variance-covariance matrix, which summarizes the shared evolutionary history between species pairs (Revell 2009) such

the lower jaw with the quadrate (large gray circle), β and σ represent the angle between the in-lever and the out-lever and between the in-lever and the line of action of the muscle, respectively. In addition to these variables, the physiological cross-sectional area (PCSA), the fiber length, and the jaw width were measured. *B*, Boxplots illustrating the bite force in the nongrazers and grazers. The lower and upper hinges correspond to the first and third quartiles. The upper whisker extends from the hinge to the largest value no further than $1.5 \times$ interquartile range (IQR). The lower whisker extends from the hinge to the smallest value at most $1.5 \times$ IQR of the hinge. Data beyond the end of the whiskers are called outlying points and are plotted individually. The size of the samples is indicated. *C*, Boxplots illustrating the mouth-closing speed in the cmd species and the noncmd species. The size of the sample is indicated. *D*, *E*, Ratio (with 95% confidence interval) of each model inputs of grazers to nongrazers (*D*) and of noncmd species to cmd species (*E*). Only the variables that were significantly different are shown. *F*, *G*, Illustrations of how gains and losses in each model input are translated into gains and losses in the biting force (*F*) and mouth-closing speed (*G*). The dashed line represents a reference biting force for the nongrazers (*F*) and a reference mouth-closing speed for the cmd species (*G*). Data underlying figure 3 have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2280gb5qh>; Olivier et al. 2020).

that an individual within a species shares an equal evolutionary history with all other members of that species. For each variable, a null distribution of F -values was generated from 10,000 Brownian motion simulations based on a phylogenetic tree built for the 29 species. Observed F -values were compared against the simulated distributions, and P summarizes the frequency of Brownian motion simulations that produced higher F -statistics than the observed data (López-Fernández et al. 2014). The time-calibrated and multigene phylogeny of Pomacentridae from Frédérich et al. (2013) was used and pruned to match the species in our data set. All the studied species were found in that phylogeny except for *Pomacentrus aquilus* and *Neopomacentrus fuliginosus*. Thus, the phyletic positions of a randomly chosen *Pomacentrus* species and of *Neopomacentrus cyanomos* were used for the missing species, respectively. Visual inspection of the residuals did not reveal severe violations of parametric assumptions (logarithmic transformation was applied, if necessary).

Differences in model inputs between the groups can be unequally translated into performance variations, as the mechanical sensitivity of output may vary among the system's underlying features (Koehl 1996; Hulsey and Wainwright 2002; Anderson and Patek 2015; Muñoz et al. 2017). We calculated a reference biting force for the nongrazers and a reference biting velocity for the cmd species, using the arithmetic means of each trait for both groups. Then, for each trait that was significantly different between the groups (grazers vs. nongrazers or noncmd species vs. cmd species), we estimated how the difference affected the modeled biting force and velocity by sequentially replacing the input values of the reference group in the biomechanical model by the mean (with 95% confidence interval) of the nonreference group.

Kinematic Study

We compared the lower jaw's closing speed calculated by the model to the kinematic data for six species, that is, three grazers (*Neoglyphidodon nigroris*, *Plectroglyphidodon lacrymatus*, and *Stegastes rectifraenum*) and three nongrazers (*Abudefduf troschelii*, *Amphiprion clarkii*, and *Chromis chromis*). *Abudefduf troschelii* and *C. chromis* lack the cmd ligament. Here, we provide new data on the grazer *P. lacrymatus* collected in a manner similar to the protocol of our previous studies (Olivier et al. 2014). The kinematic data from the other five species were retrieved from published works (Olivier et al. 2014, 2015, 2016). Specimens of *P. lacrymatus* and *S. rectifraenum* were caught in the wild and studied at field stations (Station de Biologie et Sciences Marines [BELAZA] in Madagascar and Centro de Investigaciones Biológicas del Noroeste [CIBNOR] in Mexico, respectively). As they are both grazers, we filmed

them biting filamentous algae on rubble sampled from their natural environment. Specimens of *A. troschelii* and *C. chromis* were also caught in the wild and studied at field stations (CIBNOR in Mexico and Station de Recherches Sous-marines et Océanographiques [STARESO] in France, respectively). These species do not usually feed on algae, so bites on fixed food items were studied (lumps of mussel or shrimp fixed to pliers). Specimens of *A. clarkii* and *N. nigroris* were bought from aquarium shops in Belgium and filmed while biting fixed food items. We studied at least three (up to seven) individuals per species, except for *A. troschelii* and *P. lacrymatus*, of which we caught only two and one individuals, respectively. We analyzed 141 video sequences in 21 individuals and attempted to obtain at least three analyzable video sequences per fish, although it was not always possible (table S2). Experimental and animal care protocols followed all relevant international guidelines and were approved by the ethics committee of the University of Liège (protocol no. 113).

We compared the closing velocity of the lower jaw (cm/s) predicted by the model to those observed during the B1 (AM system) and B2 (cmd system). For the lower-jaw closing velocity observed in vivo, we considered the maximum value of B1 and B2 observed for each individual. We chose the maximum value because it is actually quite difficult to elicit maximum performance given the limitations of laboratory studies (Astley et al. 2013), while the mathematical model provided the theoretical maximal performance. We performed a t -test to compare the lower-jaw closing velocity of the model and B1. Visual inspection of the residuals did not reveal violations of parametric assumptions. The difference between B2 and the modeled velocities was huge, without overlap, making a statistical test unnecessary. As the sizes of individuals studied in vivo and those dissected for model calculation were very close (7.6 ± 1.8 cm vs. 7.3 ± 1.7 cm; tables S1, S2), we did not apply size correction.

Comparisons with Other Actinopterygians

To test our assumption that the redundancy of jaw-closing systems in damselfishes provides the grazing species with an unusual combination of feeding behavior, lower jaw design, and bite velocity performance, we compared their morphology and their feeding kinematics with those of a broad sample of actinopterygians. The traditional ecomorphological view predicts that the species feeding on more elusive prey need faster bites and that species feeding on hard items (including algae) need a jaw design favoring force transmission (high closing MA; Westneat 2004). These two predictions were first checked using data from the literature. For the bite velocity, we considered

two variables: (1) the duration of mouth closing, as a proxy for speed, because this variable was available for a large set of species, and (2) the mouth-closing linear speed (cm/s). The data set for mouth-closing duration comprised 37 species belonging to 20 families and nine orders and that for mouth-closing linear speed included 28 species belonging to 14 families and eight orders (table S3). The closing lever ratio (MA) was here considered as that which corresponded to the AM bundle inserting on the dorsal part of the mandible (either on the dentary or the angular). This closing MA is easily measured and has indeed been measured in numerous fish taxa. The closing MA data set included 39 species, each belonging to a distinct family, representing 29 orders (table S4). We then collected stomach content data for all the species from FishBase (Froese and Pauly 2019). We calculated the proportion of highly elusive prey such as fish and cephalopods (nekton) and the proportion of food items requiring a forceful bite such as mollusks, hard-shelled crustaceans, and algae/plants.

Phylogenetic generalized least squares (PGLS) regression was used to test general assumptions about the relationship between (1) the bite velocity and the proportion of nekton consumed and (2) the closing MA and the proportion of hard items consumed. The Pomacentridae were not included in the analyses. The bite velocity data set was biased toward the Labridae (representing a third of the species), which can be an issue when using phylogenetic-corrected methods. Thus, we randomly selected one species per family to run the PGLS and repeated the process 1,000 times. We then considered the average of the models' parameters. When considering the bite velocity as the mouth-closing linear speed (cm/s), we used phylogenetic-size-corrected residuals (Revell 2009). All the species in the closing MA data set belonged to distinct families; we thus considered the whole set of data. The phylogenies of studied actinopterygians were retrieved via the Fish Tree of Life application programming interface using the function `fishree_phylogeny` from the R package `fishree` (Chang et al. 2018). The PGLS were run using the function `gls` from the R package `nlme` (Pinheiro et al. 2018). Finally, we compared the values of bite velocities (duration and linear speed) and closing MA of the grazing damselfishes to the other actinopterygians to test whether they followed the general trend.

Results

Comparisons of the Bite Performance between Groups

As expected, the model predicted that the AM system in grazing damselfishes provided them a more forceful bite than nongrazers (fig. 3B; table 1). All model inputs, except one, were higher in the grazers than in the nongrazers (fig. 3D; table 1). However, not all of these differences

Table 1: Results from comparing grazers to nongrazers

Models	Estimates	SE	<i>t</i> -value	<i>P</i>
Bite force (log)	1.11	.14	7.75	<.001
Jaw width	.18	.12	1.49	.191
MA A ₂	.04	.014	2.78	.012
Beta A ₂	8.71	1.39	6.28	<.001
Sigma A ₂	21.59	2.9	7.45	<.001
Length A ₂ (log)	.16	.05	3.44	.002
PCSA A ₂ (log)	1.26	.16	8.10	<.001
Fiber A ₂ (log)	.18	.05	3.73	<.001
MA A ₃	.03	.01	3.43	.002
Beta A ₃	7.56	1.43	5.31	<.001
Sigma A ₃	5.18	3.74	1.39	.177
Length A ₃ (log)	.2	.05	4.18	.001
PCSA A ₃ (log)	.53	.13	3.99	.001
Fiber A ₃ (log)	.2	.05	3.94	.001

Note: Comparison of the modeled bite force and each model input between grazers and nongrazers. The parameters of the statistical models are indicated. The estimates are the differences between the two groups. The *P* values summarize the frequency of 10,000 Brownian motion simulations based on the phylogenetic tree that produced a higher *F*-statistic than the observed data. The nongrazers are the reference group. MA = mechanical advantage; PCSA = physiological cross-sectional area.

translated to variation in biting force (fig. 3F; table S5). Higher AM PCSA, MA, and sigma A₂ values provided a more forceful bite to the grazers (fig. 3F; table S5). The model also validated our assumption that the noncmd species had a faster bite than the cmd species when only the AM system was considered (fig. 3C; table 2). The outliers in the cmd species corresponded to species larger than the others, that is, *Hemiglyphidodon plagiometopon* and *Parma microlepis*. This explains their higher mouth-closing speed (aside from these outliers, no other size differences were observed among the groups, and size-corrected analyses were not necessary; see "Material and Methods"). Seven model inputs were different between the cmd and noncmd species (fig. 3E; table 2), and the faster bite measured in noncmd species was explained by their lower MA and sigma A₂ values (fig. 3G; table S6).

Kinematic Study

There was no significant difference between the observed jaw-closing speeds in B1 and the speeds predicted by the model (fig. 4; estimate = 0.038, SE = 0.047, *t*-value = 0.815, *P* = .417). However, the predicted speed values were more than seven times slower than those observed during B2 (fig. 4; tables S1, S2). Through this comparison of in vivo and simulated performances, we demonstrate that the AM system of damselfishes cannot produce the fast mouth-closing movements observed during B2. In combination with cmd transection experiments made in

Table 2: Results from comparing species with and without the ceratomandibular (cmd) ligament

Models	Estimates	SE	<i>t</i> -value	<i>P</i>
MCS (log)	.09	.04	2.12	.031
Jaw width	-.24	.16	-1.55	.065
MA A ₂	-.07	.02	-3.92	.001
Beta A ₂	-13.42	1.66	-8.10	<.001
Sigma A ₂	-31.05	3.57	-8.71	<.001
Length A ₂ (log)	.03	.07	.46	.659
PCSA A ₂ (log)	-.80	.26	-3.04	.015
Fiber A ₂ (log)	-.06	.07	-.89	.413
MA A ₃	-.62	.29	-2.15	.011
Beta A ₃	-9.47	1.91	-4.95	<.001
Sigma A ₃	-7.15	4.92	-1.45	.226
Length A ₃ (log)	-.05	.07	-.66	.482
PCSA A ₃ (log)	-.44	.19	-2.36	.045
Fiber A ₃ (log)	-.01	.07	-.14	.881

Note: Comparisons of the modeled mouth-closing speed (MCS) and each model input between noncmd and cmd species. The parameters of the statistical models are indicated. The estimates are the differences between the two groups. The *P* values summarize the frequency of 10,000 Brownian motion simulations based on the phylogenetic tree that produced a higher *F*-statistic than the observed data. The cmd species are the reference group. MA = mechanical advantage; PCSA = physiological cross-sectional area.

previous studies (Parmentier et al. 2007; Olivier et al. 2014, 2015, 2016), the present results demonstrate that the system based on the cmd ligament is crucial in reaching such speeds.

Comparison with Other Actinopterygians

The PGLS results supported the traditional ecomorphological view predicting that species feeding on highly elusive prey have faster mouth-closing movements (fig. 5A; table 3) and that species feeding on hard items have higher MA values for mouth-closing (fig. 5B; table 3). When considering the AM system only (B1), the grazing damselfishes have slow mouth-closing movements in comparison to the range observed in actinopterygians (fig. 5C; table S3). Yet, thanks to the cmd system (B2), the damselfishes had one of the fastest mouth-closing movements known so far in actinopterygians (fig. 5C; table S3). The closing MA values of the grazing damselfishes were also among the highest recorded in actinopterygians (fig. 5D), with similar values to the Scaridae and Kyphosidae (which feed on hard items). The combination of a habit of feeding on hard items, a small and robust lower jaw (high MA), and an extremely fast bite supports our assumption that the grazing damselfishes, by circumventing an evolutionary functional trade-off, do not follow the general trend observed in actinopterygians (fig. 5).

Discussion

As is usually observed with the AM system in fish, the damselfish species with short and high lower jaws (high MA) have a more forceful bite, and species with more elongated jaws (low MA) have a faster bite. However, the presence of a single trait (i.e., the cmd ligament)

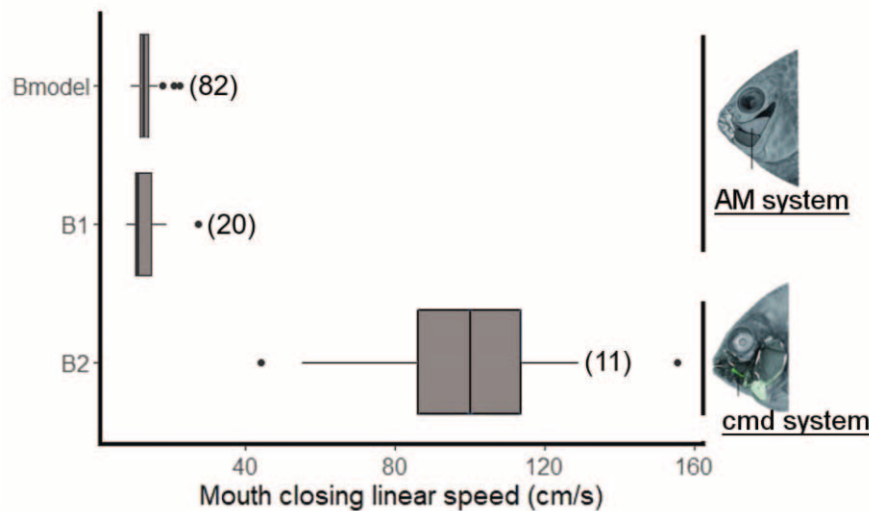


Figure 4: Bite velocity performances in the Pomacentridae. The boxplots illustrate the mouth-closing speeds predicted by the model (B model), the in vivo measured biting-1 (B1), and the in vivo measured biting-2 (B2). The lower and upper hinges correspond to the first and third quartiles. The upper whisker extends from the hinge to the largest value no further than $1.5 \times$ interquartile range (IQR). The lower whisker extends from the hinge to the smallest value at most $1.5 \times$ IQR of the hinge. Data beyond the end of the whiskers are called outlying points and are plotted individually. The size of each sample is indicated. Data underlying figure 4 have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2280gb5qh>; Olivier et al. 2020).

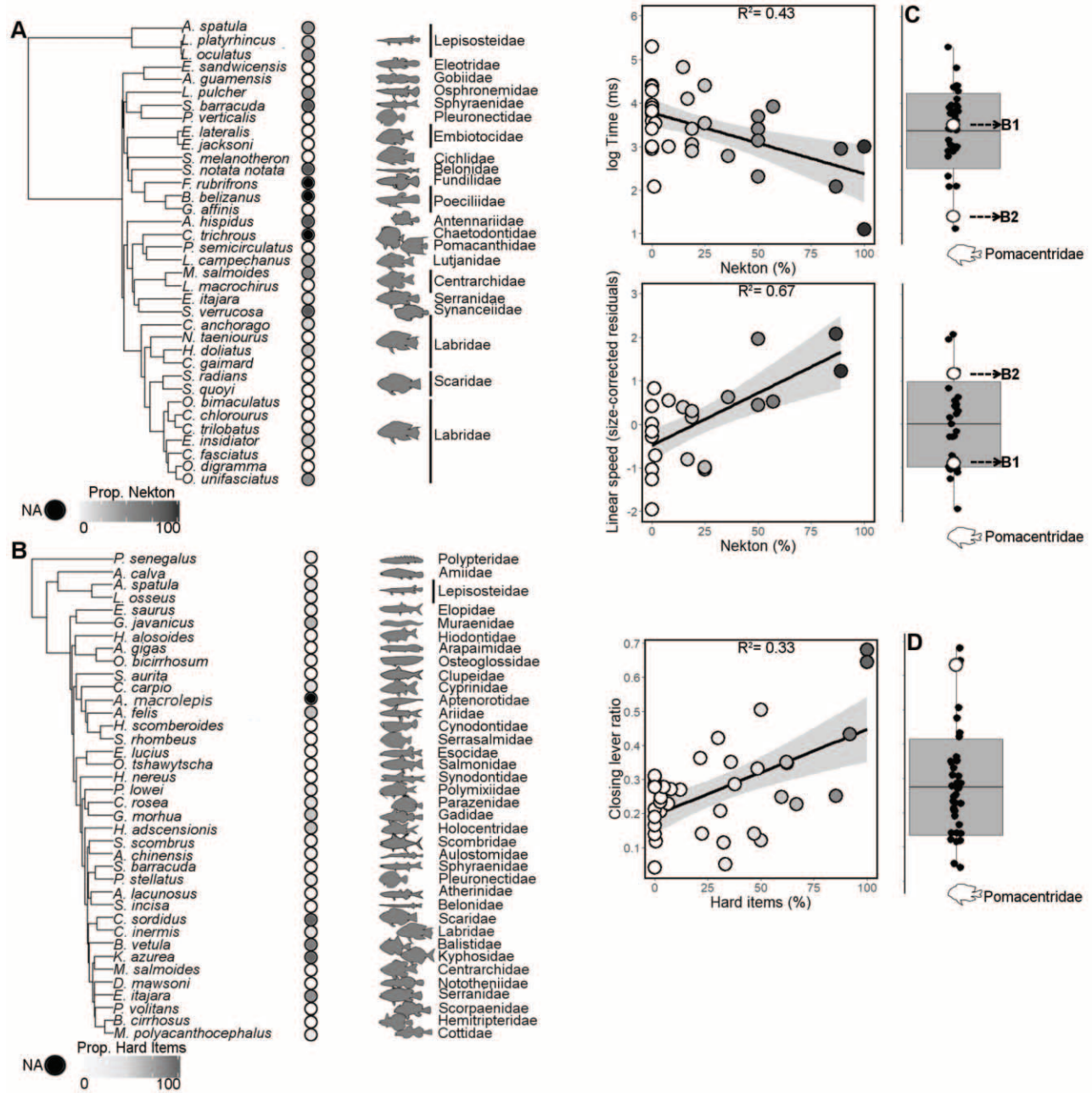


Figure 5: Bite velocity and mouth-closing lever in actinopterygians. *A*, Relationship between the bite velocity (duration and mouth-closing speed) and the proportion of nekton in the food habit. *B*, Relationship between the mouth-closing lever ratio and the proportion of hard items in the food habit. The Pomacentridae were not considered in building the models. *C*, Boxplots illustrating the mouth-closing velocity (in duration and in linear speed) in our actinopterygians sample. The lower and upper hinges correspond to the first and third quartiles. The upper whisker extends from the hinge to the largest value no further than $1.5 \times$ interquartile range (IQR). The lower whisker extends from the hinge to the smallest value at most $1.5 \times$ IQR of the hinge. The values of each studied species are indicated. The mean values reached in the grazing damselfishes during biting-1 (B1) and biting-2 (B2) are indicated. *D*, Boxplots illustrating the mouth-closing lever ratio in our actinopterygians sample. The mean value of the grazing damselfishes is shown. Data underlying figure 5 have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2280gb5qh>; Olivier et al. 2020).

Table 3: Results from fitting phylogenetic generalized least squares regressions models

Models	Estimates	SE	<i>t</i> -value	df	<i>P</i>	<i>R</i> ²
Mouth-closing duration:						
Nekton	−.0166	.0049	−3.44	1,18	.006	.43
Mouth-closing linear speed:						
Nekton	.0276	.0065	4.29	1,12	.003	.65
Mouth-closing lever ratio:						
Hard items	.0026	.0006	4.19	1,35	<.001	.33

Note: Models indicate the relationships in teleosts of the mouth-closing velocity (duration and linear speed) and the mouth-closing lever ratio with the proportion of nekton and hard items, respectively. Mouth-closing duration was log transformed. Phylogenetic size-corrected residuals were used for mouth-closing linear speed.

changes this general trend since species with a forceful bite (i.e., the grazers) were also able to have an ultrafast bite. The potential of functional complexity to mitigate functional trade-offs is an acknowledged theory (Liem 1973; Vermeij 1973; Lauder 1982; Alfaro et al. 2005; Hulsey et al. 2006), but a direct empirical example for this prediction was still lacking. Our results provide the first empirical evidence of the potential of functional complexity to circumvent functional trade-offs that have shaped organisms' evolution.

The example of damselfishes supports particularly the study of Holzman et al. (2011), where simulated levels of complexity in the cephalic morphology of centrarchid fishes showed that having different components (or systems) to create suction flow mitigated the trade-off between the capture of attached and evasive prey. In their study, simulations were required because of the lack of closely related species diverging from the others by the presence or absence of one of the different components.

The dynamic biomechanical model supports the trade-off between force and speed in the mouth-closing system of damselfishes. First, the grazers had a more forceful bite than the nongrazers, mainly due to their larger AM muscles but also because they have higher MA values and a higher insertion angle of the A_2 . Second, the predicted mouth-closing speed (AM only) was higher in noncmd species than in cmd species because of the lower MA values and the lower insertion angle of the A_2 in the noncmd species.

The model made good predictions for the mouth-closing speed observed during the B1 pattern in our kinematic data despite some simplifications, namely, (1) the A_1 bundle was not considered because it does not insert on the lower jaw; (2) the A_3 was considered to be entirely made of parallel fibers, while a small part is actually pennate (Gluckmann and Vandewalle 1999), which favored the speed transmission of the A_3 at the expense of force (Gans and de Vree 1987); and (3) the muscle properties of the Pomacentridae, such as fiber type or contractile properties, were unknown. However, we cannot rule out

that the model may underestimate the maximum performances due to the AM system because the maximal performances are rarely observed in vivo (Astley et al. 2013). Nevertheless, the mouth-closing movement was seven times faster during the B2 pattern than the modeled and in vivo B1 mouth-closing speeds.

Data collected from a large set of actinopterygians also supported the usual ecomorphological theory. Nekton feeders generally have a fast bite, while species feeding on hard items have robust lower jaws, favoring force transmission. In comparison to other clades, the grazing damselfishes have short and robust jaws, with closing MA values among the highest recorded within the actinopterygians for which information is available. Grazing damselfishes have a relatively slow bite when considering the AM system alone (B1). However, the grazing damselfishes actually have some of the fastest bites recorded so far in actinopterygians, with values equaling or even exceeding those of the fastest nekton feeders. Although the bite velocity and MA closing values were available for only a fraction of actinopterygians, our comparison considers various distinct families and orders (tables S3, S4), and the present results supported our assumption that the grazing damselfishes are outliers (fig. 5) in the evolution of teleosts by combining grazing behavior, short and robust lower jaws, and ultrafast bite.

Our study also suggests that a forceful and very fast bite is a prerequisite for farming behavior in damselfishes (fig. 6). The absence of one of these two factors—that is, the lack of the cmd ligament or a low bite force even when the cmd ligament is present (e.g., *Amblyglyphidodon* spp., *Chromis amboinensis*)—prevents the acquisition of farming behavior (fig. 6). A forceful and fast bite would seem to be a necessary but insufficient condition to adopt farming behavior, as some species with the cmd ligament and a forceful bite are not farmers (e.g., *Amphiprion akallopisos*, *Chromis dimidiata*; fig. 6). The evolutionary rise of farming behavior is likely very complex and probably also depends on other criteria, such as neuronal and ethological aspects.

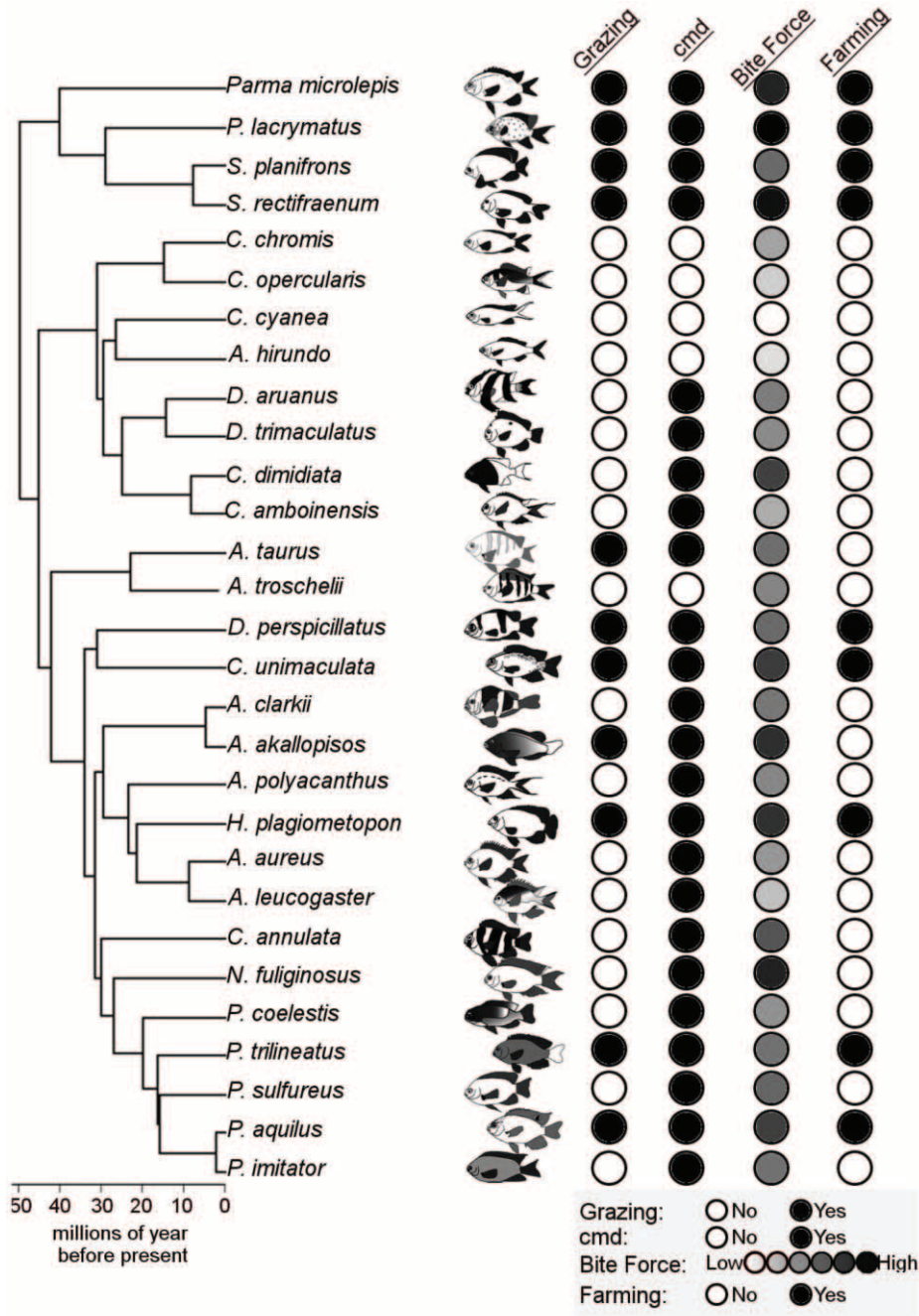


Figure 6: Phyletic relationships of the studied Pomacentridae. The grazing, ceratomandibular (cmd), and farming traits, as well as a bite force gradient, are mapped on the tree. The color gradient for the bite force has been made according to phylogenetic size-corrected residuals using the method of Revell (2009).

Other ways to circumvent the force-speed trade-off in mouth-closing movement exist within actinopterygians. The subdivision of the AM allows different bundles to favor either force or speed transmission (Westneat 2003). This was also observed in our data, where the A_2 was

shorter and had a higher MA value than the A_3 . However, our results showed that both muscles evolved to either favor force or speed transmission. Varying the bite point along the lower jaw can also mitigate the force-speed trade-off. The barracuda *Sphyraena barracuda*, a top predator,

has elongated jaws and was one of the faster biters in our data set. The closing MA, when measured at the rostral tip of the lower jaw, is low and therefore increases the transmission of speed (Westneat 2004). However, barracudas have a long row of shearing teeth that allow them to bite their prey at the posterior corner of the lower jaw, where the MA—and, thus, the bite force—is much higher (Grubich et al. 2008). This combination enables barracudas to have not only a very fast bite to capture their prey but also a forceful bite to slice their prey (Porter and Motta 2004; Grubich et al. 2008). This trade-off mitigation, however, does not apply to farming damselfishes that need a forceful and fast bite at the rostral tip of their lower jaw, where filamentous algae are seized.

Few concepts in evolutionary biology have generated as much ambiguity and controversy as that of key innovation (Rabosky 2017). A key innovation was recently defined as a trait (or a set of traits) that allows a lineage to interact with the environment in a fundamentally different way (Stroud and Losos 2016) and increases the total diversification—but not necessarily the diversification rate—of the parent clade (Rabosky 2017). There is also consensus that a key innovation requires the presence of an ecological opportunity to allow the clade to diversify (Stroud and Losos 2016; Wainwright and Price 2016) and that this ecological opportunity can be available in the habitat or the clade can create its ecological opportunity via alterations to the physical environment (i.e., via ecosystem engineering; Jones et al. 1994; Stroud and Losos 2016). The cmd ligament in damselfishes clearly meets the first part of the key innovation definition, as it allows the lineage to interact with the environment in a fundamentally different way since it enables farming, a behavior that creates an ecological opportunity by altering the physical environment. The second part of the key innovation definition is more controversial for damselfishes. Does the cmd ligament increase the total diversity of the clade? Noncmd species are less species rich, and all are zooplanktivorous, while an iterative radiation among three trophic guilds is observed in cmd species (Frédérich et al. 2013, 2014). The noncmd species are also functionally less diversified, as they can perform only one biting mode (B1; Olivier et al. 2016). In this sense, the cmd ligament seems to increase the diversity. On the other hand, innovations can also have constraining effects. Pharyngognathy in fishes opened up ecological opportunities in the form of diets that involve tough and hard prey, but this came at the cost of diets that involve swallowing large whole prey (Mcgee et al. 2015). In damselfishes, the secondary loss of the cmd ligament removes some evolutionary constraints on buccal jaws and associated body shapes (Frédérich et al. 2014), as the noncmd species occupy a morphofunctional space distinct from cmd species

(Frédérich et al. 2014; Olivier et al. 2017). The noncmd species also produce acoustical signals that are distinct from those of the cmd species (Frédérich et al. 2014); these signals are a major component of communication in damselfishes used in reproductive and agonistic behaviors (Parmentier et al. 2016). The coupling between the lower jaw and the hyoid bar can also alter the anterior-to-posterior wave necessary for suction feeding because it may affect the timing of lower-jaw depression relative to hyoid depression (Day et al. 2005; Bishop et al. 2008), and this constraint may require future investigations. Thus, the secondary loss of the cmd ligament also seems to have increased the diversity of the clade. To date, we cannot state whether the cmd ligament can be considered as a key innovation, but this trait has certainly shaped the ecological diversification of this reef fish family.

Conclusions

Trade-offs can be circumvented by the acquisition of an evolutionary novelty that allows previously antagonistic tasks to be optimized. The cmd is an evolutionary novelty that duplicated the mouth-closing system in damselfishes. This functional redundancy allowed damselfish to circumvent the trade-off between force and velocity in the lower jaw of fish, widening the feeding repertoire of herbivory in teleosts, and, in turn, likely allowing the damselfishes to colonize the farming ecological niche.

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Statement of Authorship

D.O. and B.F. designed the study. D.O. and B.F. collected and analyzed the data. S.W. developed the mathematical biting model. D.O., B.F., E.P., and S.W. interpreted the data and wrote the manuscript. All the authors approved the final manuscript.

Data and Code Availability

Data and R code to run all analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2280gb5qh>; Olivier et al. 2020).

APPENDIX

Biomechanical Biting Model

The morphological data collected during this study (see “Material and Methods”) served as inputs in a mouth-closing model, which calculates angular motion of the lower jaw based on the dynamic equilibrium of the external torques acting on the system. The model used in the current study is a modified version of a previously published model that has been validated for catfishes (Van Wassenbergh et al. 2005). The lower jaw adduction is modeled as a rotation of a half-circle (cmd species) or a half-elliptic (noncmd species) plate scaled to the lower jaw dimensions. Upon rotation of this plate, a certain amount of water surrounding it will be put in motion as well. Therefore, the inertia of the rotating lower jaw is increased by including an added mass component that has the volume of the half-spheroid/ellipsoid comprising the half-circle/ellipse surface. At each point along the length axis of the lower jaw, the radius of this half-spheroid/ellipsoid equals the half width of the half-circle/ellipse.

Upward rotation of the lower jaw is caused by contraction of the jaw adductor muscles. The model calculates the instantaneous angular acceleration (α) of the lower jaw by using the following equation of motion:

$$I\alpha = M_m + M_d, \quad (\text{A1})$$

where I is the moment of inertia of the lower jaw and added mass with respect to the axis of rotation, and M_m and M_d are the moments from, respectively, the jaw muscle activity and hydrodynamic drag. In contrast to the original model, no additional resistance due to positive pressure inside of the buccal cavity at the end of the mouth-closing phase was included: due to the observed, continued expansion of the buccal cavity during jaw closing (Olivier et al. 2015, 2016), pressure will almost certainly not become positive during this period in damselfishes. The instantane-

ous moment of force generated by the jaw muscles (M_m) is calculated by

$$M_m = \sum F_m \sin \sigma L_{in}, \quad (\text{A2})$$

where F_m is the instantaneous force along the line of action of one of the jaw adductors and σ the instantaneous (gape-dependent) inclination of the jaw muscle with respect to the in-lever with length L_{in} . The contractile properties determining the instantaneous force produced by the jaw muscle (F_m)—namely, the force-velocity dependence (Hill curve) and force-length dependence (optimal sarcomere overlap for a relevant range of gape angles)—are modeled as described in the original model.

Maximal bite force is calculated from the static equilibrium of forces at the tip of the lower jaw:

$$\text{bite force} = \frac{M_m}{\text{out-lever length}}, \quad (\text{A3})$$

where M_m is now the moment of force from the different jaw adductors in an isometric, fully activated state. A maximal muscle stress of 19 N cm^{-2} , measured for an acinopterygian *adductor mandibulae*, was used (Van Wassenbergh et al. 2007).

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