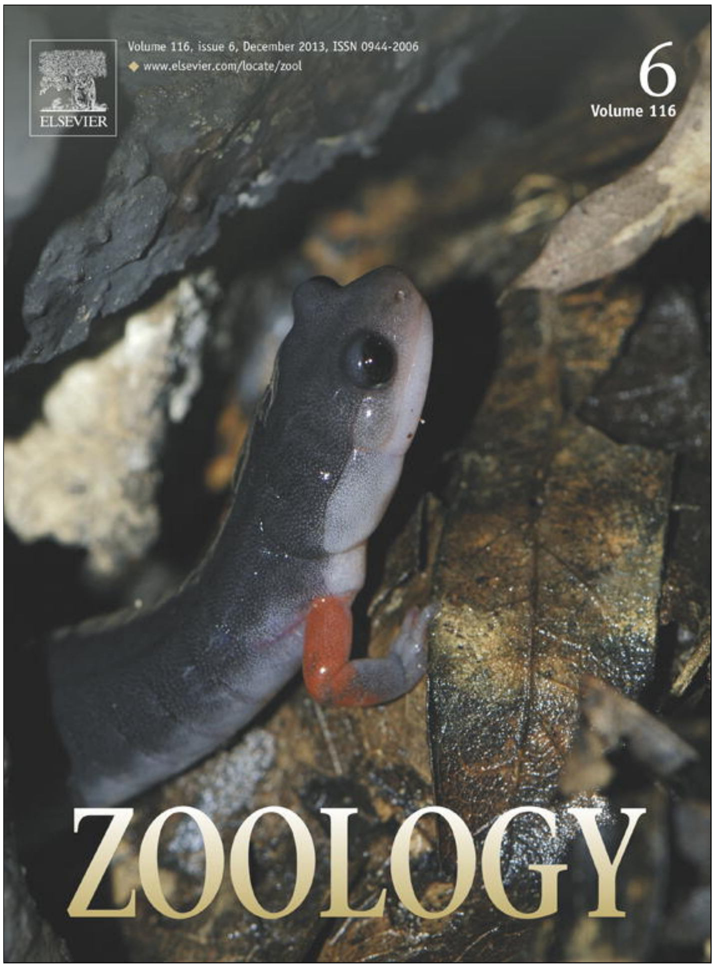
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A forceful upper jaw facilitates picking-based prey capture: biomechanics of feeding in a butterflyfish, *Chaetodon trichrous*

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ABSTRACT

Biomechanical models of feeding mechanisms elucidate how animals capture food in the wild, which, in turn, expands our understanding of their fundamental trophic niche. However, little attention has been given to modeling the protrusible upper jaw apparatus that characterizes many teleost species. We expanded existing biomechanical models to include upper jaw forces using a generalist butterflyfish, *Chaetodon trichrous* (Chaetodontidae) that produces substantial upper jaw protrusion when feeding on midwater and benthic prey. Laboratory feeding trials for *C. trichrous* were recorded using high-speed digital imaging; from these sequences we quantified feeding performance parameters to use as inputs for the biomechanical model. According to the model outputs, the upper jaw makes a substantial contribution to the overall forces produced during mouth closing in *C. trichrous*. Thus, biomechanical models that only consider lower jaw closing forces will underestimate total bite force for this and likely other teleost species. We also quantified and subsequently modeled feeding events for *C. trichrous* consuming prey from the water column versus picking attached prey from the substrate to investigate whether there is a functional trade-off between prey capture modes. We found that individuals of *C. trichrous* alter their feeding behavior when consuming different prey types by changing the timing and magnitude of upper and lower jaw movements and that this behavioral modification will affect the forces produced by the jaws during prey capture by dynamically altering the lever mechanics of the jaws. In fact, the slower, lower magnitude movements produced during picking-based prey capture should produce a more forceful bite, which will facilitate feeding on benthic attached prey items, such as corals. Similarities between butterflyfishes and other teleost lineages that also employ picking-based prey capture suggest that a suite of key behavioral and morphological innovations enhances feeding success for benthic attached prey items.

1. Introduction

The anterior jaw apparatus of teleosts, or derived bony fishes, provides insight into the fundamental mechanisms that underlie vertebrate evolution (Lauder, 1982) and is tractable for field, laboratory, and theoretical studies of anatomy, physiology and behavior. In fact, cranial anatomy can be used to construct a biomechanical model of the teleost feeding mechanism that accurately estimates bite force and other performance parameters for individuals feeding in the wild (Westneat, 2003, 2004; Wainwright et al., 2004; Hulsey and García de León, 2005). However, because the skull is composed of more than 20 kinetic elements and there are multiple ways these elements can be coordinated, the dynamic movements of the cranial bones of teleosts present a challenge for biomechanical modeling (Westneat, 2004).

One way to simplify biomechanical modeling of such a complex system is to focus solely on the lower jaw. Because the lower jaw closes the mouth in many teleosts, current biomechanical models of teleost bite forces only evaluate the velocity and force consequences of lower jaw movements and do not consider potential force production by the upper jaw (see Westneat, 2003). In fact, if the mandible (lower jaw) is depressed and then elevated with no premaxillary (upper jaw) protrusion, or if the upper jaw is protruded but does not contribute to mouth closing, or if no force is applied to the prey by the upper jaw, then a biomechanical model that only incorporates lower jaw components *can* accurately predict performance parameters (Westneat, 1994). However, in some teleosts, the tooth-bearing upper jaw, or premaxilla, projects (or protrudes) anteriorly during prey capture and contributes to mouth closing (Ferry-Graham et al., 2001;

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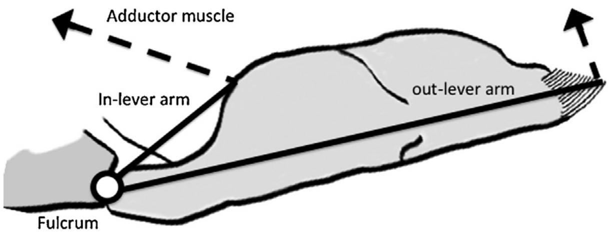


Fig. 1. The lower jaw of a teleost fish can be considered a third order lever with a fulcrum (open circle) at the articulation with the jaw joint (suspensorium). The mechanical advantage of the lever is quantified by measuring the in-lever and out-lever (black lines) relative to the insertion of the jaw-closing muscle (black dotted line); arrows indicate the direction of force into the system (via the muscle) and out of the system (through the anterior teeth).

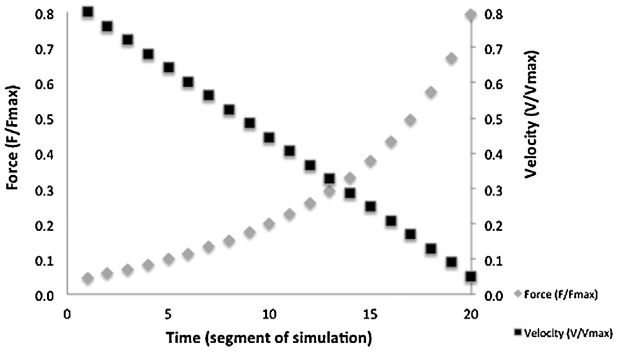


Fig. 2. The Hill equation quantifies the non-linear length–tension relationship seen in vertebrate skeletal muscle. For jaw closing in teleost fishes, when the muscle exerts force on the maximally abducted lower jaw (shown here as time = 0) the muscle contracts with a high shortening velocity but can only produce low force. As the jaw closes (and nears time = 20), shortening velocity decreases, but force produced by the muscle increases.

Konow and Bellwood, 2005), which creates a more complicated mechanical system.

In fact, the upper jaw protrusion that characterizes many successful teleost lineages may have evolved to facilitate complex feeding behaviors. For example, very small food items can be difficult to scrape or detach from hard substrata (Purcell and Bellwood, 1993) and the challenge of removing such items may have led to an increase in complexity of the jaws that, in turn, allows refined jaw movements and increased dexterity (Hernandez et al., 2008). In some fishes that employ these feeding strategies, the upper jaw protrudes anteriorly and ventrally to apply force directly to the prey (Ferry-Graham et al., 2008). In such cases, the added element of the mobile, forceful upper jaw renders the standard biomechanical models (those that consider only the lower jaw elements) unsuitable for predicting overall performance of the jaws.

For the present study, a representative species from the butterflyfishes (Chaetodontidae) was selected to assess the ramifications of forceful upper jaw protrusion on prey capture behavior. Many butterflyfish species employ a picking-based method of prey capture, wherein they grip (using the tips of the upper and lower anterior jaws) and then tear or bite off pieces from attached prey items, including polychaetes, nemerteans, corals, ascidians, echinoids, and hydroids (Ferry-Graham et al., 2001). However, when feeding on mobile prey in the water column, a suction-bite feeding mode (henceforth abbreviated here as "suction feeding" or "suction") may be employed (Ferry-Graham et al., 2001), in which buccal suction draws the prey into the oral cavity where it is then trapped between the tips of the upper and lower anterior jaws. These two prey capture modes (picking vs. suction) provide an opportunity to consider the role of the upper jaw in facilitating bite forces and enable us to examine the mechanical trade-offs associated with different feeding modalities. For example, an increase in bite force should come at a direct cost to jaw velocity and possibly to other performance traits as well (Holzman et al., 2011).

Biomechanical models that incorporate jaw lever mechanics can be used to assess these potential trade-offs between force and velocity during prey capture. A commonly used biomechanical model, originally proposed by Westneat (2003), considers the actions of the major jaw-closing muscles (two subdivisions of the adductor mandibulae muscle complex) on the lower jaw (or mandible) during prey capture. A brief description of the original model is given here; details of modifications to the model made in this study are given in Section 2. In Westneat's model, jaw-closing muscles act on the lower jaw to create a third order lever (Fig. 1). Anatomical measurements used as input for the model include the in-lever for each muscle (the distance from the muscle attachment on the jaw to the fulcrum at the junction of the lower jaw with a cranial structure called the suspensorium), the out-lever of each muscle (distance from the fulcrum of each lever to the tip of the lower jaw), and the length and mass of each muscle. Further, the distance from the origin of the muscle to the fulcrum is used to determine the angle (α) between the muscle and the in-lever arm; as this angle changes during jaw closing, the effective mechanical advantage of the lever also changes.

These anatomical measurements are used in combination with the Hill equation (Hill, 1938) for non-linear length–tension properties of skeletal muscles ($F = (1 - v)/(1 + v/k)$, where F is force, v is velocity and k is a constant (−0.025) to estimate dynamic properties of the jaws throughout jaw closing (Fig. 2). The model assumes that jaw-closing muscles are fast glycolytic (type IIb) skeletal muscles that are able to achieve a maximum contraction velocity ($V_{\max}$, or maximum unloaded contraction speed) of 10 lengths per second. However, the model also assumes that these muscles do not reach their peak velocity, but instead reach a $V/V_{\max}$ between 0.8 and 0.05 (that is, a range of values between 5% and 80% of maximum velocity divided equally between each segment of simulation; Fig. 2), which will result in a similar range of force values ($F/F_{\max}$). The model also assumes that maximum velocity occurs when the jaw is beginning abduction (from a maximally adducted position) and maximum force is produced when the teeth of the upper and lower jaws come into contact with one another (at the end of jaw adduction). Another input for the model is the physiological cross-sectional area of each muscle ($\mathrm{PCSA} = m \times \cos(\theta)/(\rho L)$, where ρ is the muscle density (g/cm^3), L is the fiber length (cm), and θ is the angle (°) of pennation of the muscle; PCSA is multiplied by the maximum isometric stress of the muscle (K) to estimate the maximum force ($F_{\max} = \mathrm{PCSA} \times K$) that each muscle can produce. However, the model also assumes that a muscle does not reach peak force during jaw closing. To calculate how much force (N) is exerted on the lever, the acting force (F_{act}) for a given muscle is estimated by multiplying the maximum force the muscle can exert by the percent of force the muscle exerts during that segment of jaw closing (as predicted by the Hill equation) with the equation: $F_{\mathrm{act}} = F_{\max} \times F/F_{\max}$. Once the force acting on the lever (F_{act}) is determined, the force out of the lever (F_{out}) is calculated by multiplying the input force by the mechanical advantage ($F_{\mathrm{out}} = F_{\mathrm{act}} \times \sin(\alpha) \times \mathrm{MA}$, where MA is the mechanical advantage of the lever, or the in-lever divided by the out-lever and α is the angle between the in-lever and the muscle).

To generate dynamic model output, the entire jaw closing (or adduction) interval is modeled by dividing jaw closing into twenty equal time segments. Contraction duration (ms) per segment can be calculated as a percentage of muscle contraction for each segment of jaw closing (that is, $t = \%\ \mathrm{contraction}/(V_{\max} \times V/V_{\max})$) and summing the contraction durations/segment yields the total time to jaw closing. Angular velocity (°/ms) of the jaw during closing is calculated as the difference in jaw rotation angle at the start and

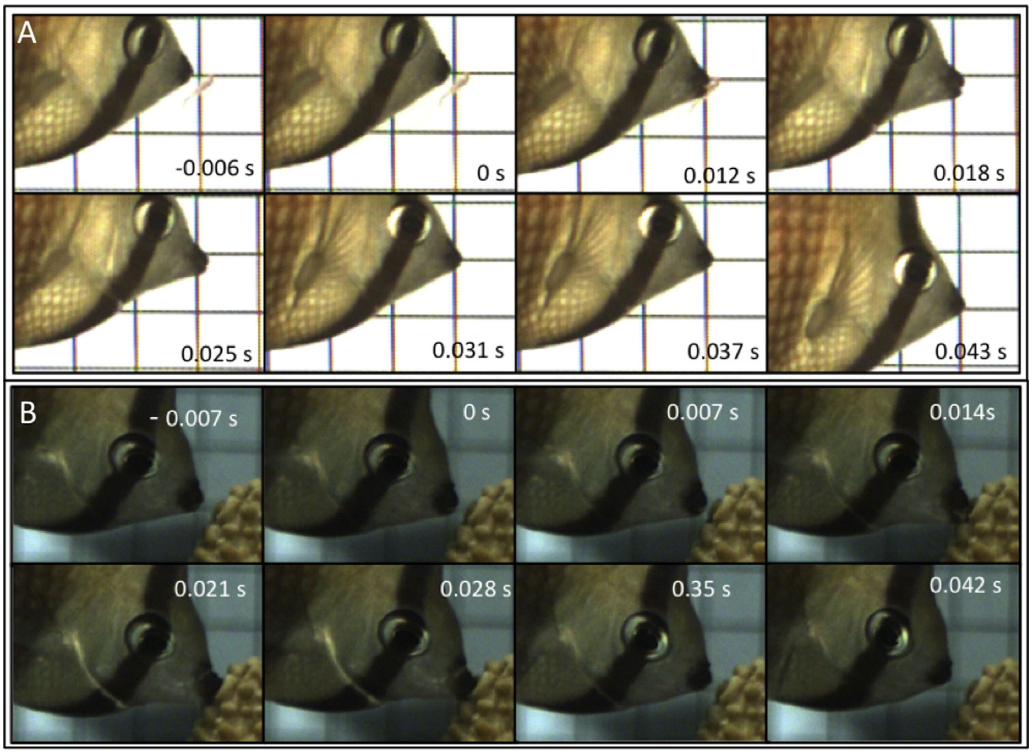


Fig. 3. *Chaetodon trichrous* modulate feeding behavior when presented with different prey types. Sequential frames have been selected and cropped from representative video sequences and time (in s) is given in the lower right corner of each panel, where time = 0 is the frame just before the onset of rapid mouth opening. (A) *C. trichrous* employ suction feeding when procuring brine shrimp from the water column. (B) *C. trichrous* employ picking-based feeding when procuring coral polyps from the substrate. During picking, the upper jaw directly contacts the coral at approximately the time of maximum gape (0.021 s).

finish of each segment of jaw closing, divided by the total time of that segment of jaw closing ($U_{\mathrm{ang}} = r/t$, where r is total jaw rotation over the course of each time segment).

In the present study, we use high-speed image analysis and biomechanical modeling to examine the feeding behavior of a representative butterflyfish species, *Chaetodon trichrous*, when capturing two different prey types: free-floating prey in the water column and benthic attached prey. Kinematic analysis of these feeding events and a morphological analysis of cranial anatomy are used to quantify feeding behaviors during different feeding modes, examine the mechanism that underlies upper jaw protrusion, and reconfigure an existing biomechanical model to incorporate forces produced by both the upper and lower anterior jaws during feeding. With these data and analyses, we address a suite of related questions: How does the highly modified cranial anatomy of *Chaetodon* (see Motta, 1982) produce upper jaw protrusion? Does upper jaw protrusion contribute to overall bite force in *Chaetodon*? Does premaxillary protrusion change when fish are presented with different prey types? If so, how do changes in the magnitude of jaw movements affect upper jaw bite force? We hypothesize that *C. trichrous* alter key aspects of the jaw movements to increase bite force when feeding on more challenging prey items (such as benthic attached prey), and that these kinematic changes serve to enhance the production of a forceful bite during jaw adduction.

2. Materials and methods

2.1. Fish acquisition and care

Live specimens ($N = 5$; mean standard length (SL) = 8.8 cm, range SL: 7.4–10.2 cm) of *Chaetodon trichrous* (Günther, 1874) were obtained from a commercial vendor (www.liveaquaria.com). Individuals were housed in a recirculating salt water system consisting of a common filter/sump and four individual 75-l aquaria. Each aquarium was divided into two compartments and each compartment housed one individual. Aquaria were maintained at 25 °C and provided with a 12L:12D light cycle. Fish were maintained on a variety of commercially available food items, including TetraMin flake food (Tetra, Melle, Germany), frozen brine shrimp, bloodworms, and Hikari Mega-Marine diet (Hikari USA, Hayward, CA, USA).

Prior to feeding trials, the individual to be tested was removed from the holding tank, placed in a 56-l filming tank, and allowed to acclimate for a minimum of 2 h. Fish were not fed during the 2 h preceding the trial; longer fasting periods were not necessary as fish fed readily.

All procedures used to maintain fish and to conduct the experiments described in Sections 2.2 and 2.3 were conducted in accordance with NAU IACUC 09-001.

2.2. Kinematics analysis of feeding behavior

A high-speed digital video system (Phantom V5; Vision Research, Inc., Wayne, NJ, USA) recording at 800 frames per second was used to capture images of feeding events for individuals of *C. trichrous*. Fish were offered brine shrimp adults (*Artemia* sp.) to elicit suction feeding in the water column and live, hard corals (*Montipora* spp.) to elicit picking-based feeding events from the substrate (henceforth abbreviated as "picking"). Feeding events were recorded from a lateral view (that is, encompassing the lateral aspect of the fish), and we only analyzed sequences in which the fish remained perpendicular to the camera during the entire gape cycle (Fig. 3). Four feeding events per individual, per prey type, were recorded (yielding a total of eight video sequences for each individual), and mean values were calculated for a given food type for each individual.

Table 1
Mean values (± SEM) for kinematic variables as measured from high-speed digital video images of *Chaetodon trichrous* individuals feeding in the laboratory (N = 4 for suction-feeding, N = 5 for picking). According to discriminant function analysis, depression of the mandible, jaw strike velocity, strike time, and premaxilla protrusion (indicated in the table by an asterisk) characterize the two prey capture modes.

	Suction feeding (N = 5)		Picking (N = 4)	
	Mean	SEM±	Mean	SEM±
Mandible depression (°)*	11.8	3.06	28.02	4.74
Jaw strike velocity (cm/s)*	96.77	11.92	32.37	4.99
Strike time (s)*	0.0096	0.001	0.018	0.001
Premaxilla protrusion (cm)*	0.637	0.122	0.352	0.042
Maximum gape (cm)	0.232	0.048	0.127	0.012
Change in premaxilla angle (°)	7.97	1.43	10.8	3.08
Time of prey capture to end of gape cycle (s)	0.025	0.002	0.024	0.003
Maximum gape angle (°)	16.95	5.19	37.23	14.7
Angle of attack (°)	23.4	16.06	24.72	13.24
Strike distance (cm)	1.43	0.54	0.55	0.123

A suite of kinematic variables was measured from the resulting digital image sequences using the computer software DIDGE (Cullum, 2003). To calculate these variables, points (with x, y coordinates) were manually placed on anatomical landmarks in each frame of the video sequence. From the change in the position of the landmark points over time (number of frames/frame rate), the following kinematic variables were calculated: (1) mandible depression (the maximum ventral movement of the tip of the lower jaw through the strike measured as net degrees of rotation, (2) premaxilla protrusion (the net anterior linear displacement of the premaxilla from onset of strike to prey capture), (3) maximum gape (the maximum linear distance between the tip of the premaxilla and the tip of the dentary, subtracted from the minimum distance to produce net maximum gape), (4) maximum gape angle (an angle defined by the tip of the premaxilla, the premaxilla/dentary junction, and the tip of the dentary) produced during the feeding event, (5) time of prey capture to end of the gape cycle (the time interval between prey capture to the minimum gape after the strike), (6) strike distance (the distance between the fish and the prey at the onset of the strike), (7) strike time (the time interval between the onset of the strike to the time the prey was captured; here, the time when the prey was grasped between the upper and lower jaws), (8) angle of attack (orientation of the long axis of the fish, as measured from the tip of the snout to the caudal peduncle, relative to a line parallel to the horizontal plane of the substrate), (9) strike velocity (strike distance divided by strike duration), and (10) premaxilla angle (the change in the angle defined by the anterior tip of the premaxilla, a fixed point on the frontal bone, and a fixed point on the body near the pectoral fin).

We employed discriminant function analysis (SPSS Statistics v. 19; IBM Corp., Armonk, NY, USA) to determine if picking events were quantitatively distinct from suction events when the entire kinematic dataset was considered. This analysis also allowed us to determine which variables were most important in categorizing feeding events by feeding mode (suction or picking) (Table 1). The null hypothesis for the DFA analysis was that all feeding events are indistinguishable from one another.

2.3. Biomechanical modeling

Preserved specimens of *C. trichrous* were examined through dissection, physical manipulation, and X-ray photography; cleared and stained specimens were also examined. A suite of anatomical measurements (see Fig. 4 and Table 2) were taken from three specimens and used as input for the biomechanical model. All measurements outlined here for the lower jaw were taken in the same manner as described by Westneat (2003). However, because we refined his biomechanical model to include the contribution of the upper jaw elements, we added a suite of anatomical measurements

Table 2
Definition of the morphological measurements taken from preserved specimens of *Chaetodon trichrous* and entered into the biomechanical bite force model. Measurements described here are also illustrated in Fig. 4.

Measurement #	Morphological measurement description
1	Distance from the articulodentomaxillary (also termed the “primordial ligament”) to the premaxilla/maxilla apposition (i.e. the point where the premaxilla and maxilla make contact at the premaxillary condoyle of the maxilla; see Lauder, 1982)
2	Distance from the origin of the adductor mandibulae (AM) 1 muscle to the premaxilla/maxilla apposition
3	Distance from the insertion of the AM1 muscle to the premaxilla/maxilla apposition
4	Distance from the insertion of the AM2 muscle on the maxilla to the premaxilla/maxilla apposition
5	Distance from the insertion of the articulomaxillary ligament on the articular to the articular/quadrate joint
6	Distance from the insertion of the AM3 muscle to the articular/quadrate joint
7	Distance from the articular/quadrate joint to the interoperculomandibular ligament
8	Distance from the articular/quadrate joint to the tip of the lower jaw
9	Distance from the premaxilla/maxilla apposition to the tip of the upper jaw
10	Length of the AM1 muscle
11	Length of the AM2 muscle
12	Length of the AM3 muscle
13	Distance from the origin of the AM2 muscle to the premaxilla/maxilla apposition
14	Distance from the origin of the AM2 muscle to the articular/quadrate bone
15	Distance from the origin of the AM3 muscle to the articular/quadrate joint
16	Distance from where the inner articulomaxillary ligament fuses with the AM2 muscle to the premaxilla/maxilla apposition
17	Length of the inner articulomaxillary ligament
18	Length of the outer articulomaxillary ligament
19	Distance from the insertion of the outer articulomaxillary ligament on the articular to the origin of the AM2 muscle
20	Insertion of the inner articulomaxillary ligament on the maxilla to the origin of the AM2 muscle
21	Distance from where the outer articulomaxillary ligament fuses with the AM2 muscle to the articular/quadrate joint
22	Distance from the articular/quadrate joint to the articulodentomaxillary ligament
23	Distance from the premaxilla/maxilla apposition to the articular/quadrate joint
24	Mass of the AM1 muscle
25	Mass of the AM2 muscle
26	Mass of the AM3 muscle

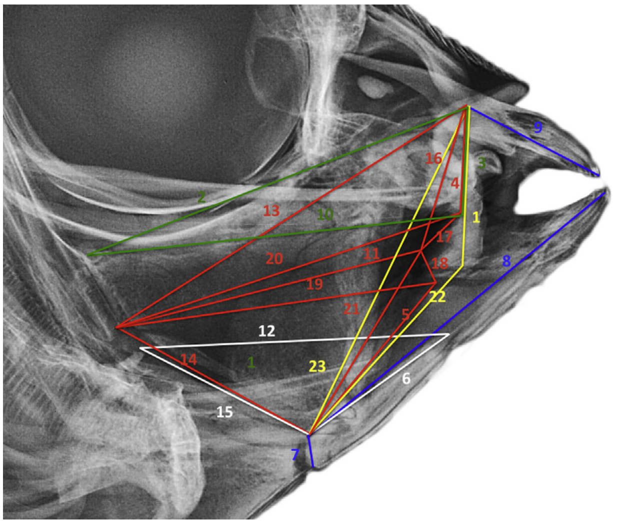


Fig. 4. Measurements taken from preserved specimens were used to generate the biomechanical model used in this study. Here, an X-ray of *Chaetodon trichrous* (Smithsonian Museum of Natural History; USNM 392506) illustrates how anatomical proportions were quantified. Green lines represent distances associated with the AM1 in-lever, red lines represent distances associated with the AM2 in-levers (to both the upper and lower jaws), white lines represent distances associated with the AM3 in-lever, yellow lines represent distances associated with the mandible/maxilla in-lever, and blue represents jaw out-levers and the jaw-opening lever. Numbers correspond to the itemized description of these measurements as provided in Table 2.

for the levers and muscle dimensions associated with the upper jaw.

The model used here is modified from the equations developed by Westneat (see Westneat, 2003 for a complete description of the model) and calculated iteratively in a spreadsheet program (Microsoft Excel; Microsoft Corp., Redmond, WA, USA) Because Westneat's model considered only the lower jaw mechanics, additional elements were added to generate a new component that quantifies the movements and forces of the upper jaw. An additional element was also added to the lower jaw model, one that considers the potential force exerted by the mandible on the maxilla, because this element may have an effect on the forces produced by both the lower and upper jaws (Fig. 5).

In Westneat's original model and in the revised model used here, the jaw-closing event is subdivided into time segments (20 in total) and the biomechanical parameters associated with the model (e.g., bite force, effective mechanical advantage, duration of jaw closing, angular velocity) are calculated for each time segment and, when appropriate, summed to determine the total value for the feeding event. A single model simulation of jaw closing was generated for each individual *C. trichrous* on each prey type and the results were averaged across all individuals. We also followed the assumptions of Westneat (2003) for parameters related to the physiological properties of the jaw-closing muscles; density was assumed to be 1.05 g/cm^3, fiber type was assumed to be fast glycolytic (type IIb) with a maximum contraction velocity of 10 lengths per second, and maximum isometric stress was assumed to be 200 kPa during contraction. During the simulations, we used an empirically derived value (taken from the kinematic analysis) for duration of jaw opening (0.015 s).

In the model, the jaws are considered as a series of levers whereby the force entering into the system is applied to an in-lever by a given muscle, the lever rotates around a fulcrum (the point about which the bone pivots), and force is transferred through the out-lever to the anterior tip of the jaws (Figs. 1 and 5). As was done in the original model (Westneat, 2003), all parameters and outputs reported here (including force) are given for a single side of the

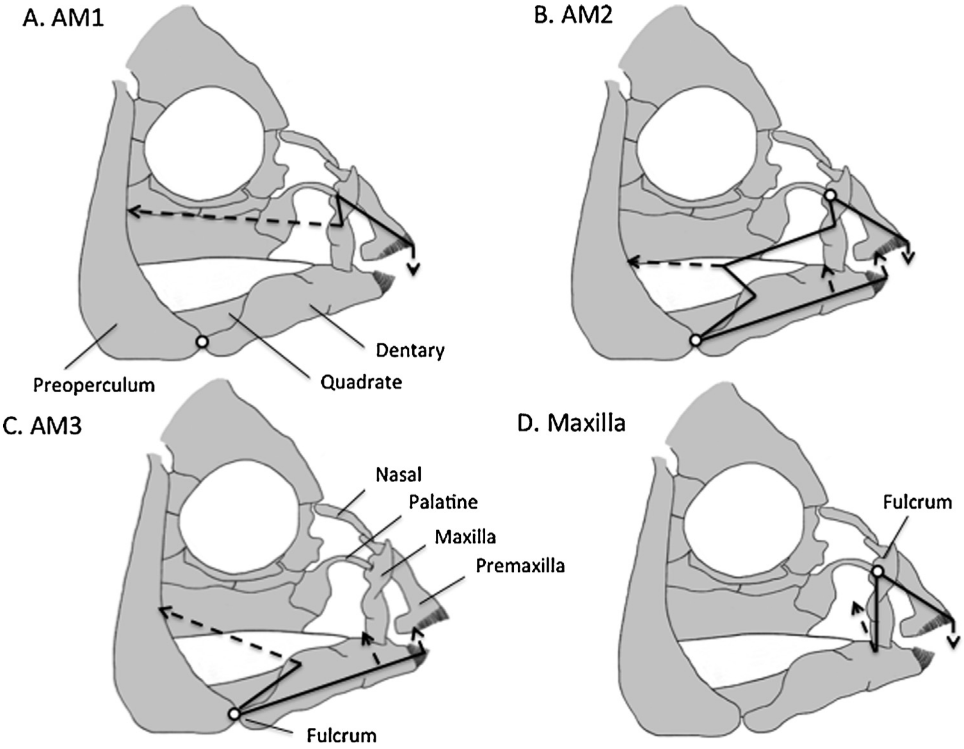


Fig. 5. The jaws of *Chaetodon trichrous* can be considered third order levers that produce force at the jaw tips during closing. The skull of *C. trichrous* is shown here to illustrate the input (dashed arrows) and output (solid arrows) for: (A) the lever associated with the AM1 (first division of the adductor mandibulae, or AM) muscle as it acts on the maxilla/premaxilla; (B) the lever associated with the AM2 (second division of AM) muscle as it acts to close both the upper and lower jaw through its connections with the mandible and maxilla; (C) the lever associated with the AM3 (third division of the AM) muscle as it acts on the mandible; (D) the lever created by the upward force of the maxilla on the mandible as the AM2 and AM3 act on the mandible and transmit force to the upper jaw. All in/out-levers are represented by solid black lines.

jaw, each muscle–lever interaction is computed independently of all others, and all biomechanical parameters are calculated for a given lever.

Following Westneat (2003), the Hill equation for non-linear length–tension properties of muscles was used to calculate all parameters associated with jaw closing dynamics. This equation is used in all calculations to establish the force/velocity relationship for each muscle. Further, following Westneat (2003), the following assumptions are made: maximum velocity (V_{max}) for fish jaw muscles is 10 lengths per second, the range of V/V_{max} (or % maximum velocity) is between 0.05 and 0.8 of V_{max} (under the assumption that muscles rarely reach V_{max}, and there will be a high jaw velocity/low bite force at the onset of mouth closing and a low jaw velocity/high bite force at the end of mouth closing. Using these parameters, we can predict the velocity and force of jaw closing for each of the 20 simulated time segments of the bite. Additional parameters outlined in Westneat (2003) and calculated here according to his methods include physiological cross-sectional area of muscle, maximum isometric force per unit area of muscle, percent muscle contraction, muscle force acting on each lever, rotational torque as the lever pivots on the fulcrum, jaw rotation, time of jaw closing, bite force at the tip of the jaws, effective mechanical advantage, closing duration, and angular velocity (see Westneat, 2003 for a complete description of these calculations).

As outlined above, we generally followed the model outlined by Westneat (2003); however, we made the following changes to the model's equations to accommodate the highly modified anatomy of *C. trichrous* and the corresponding changes in lever mechanics.

The standard equation used to estimate force of a muscle acting on a lever is:

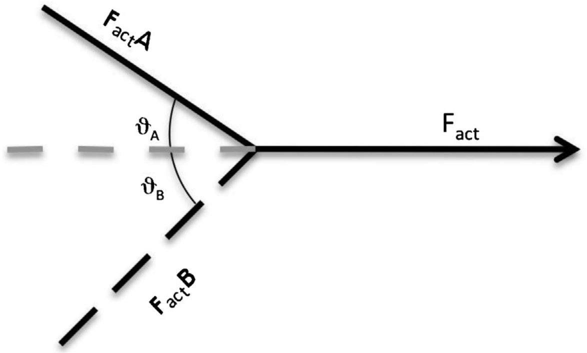
$$F_{act} = F_{max} \times F,$$

where F_{act} is the force applied by the muscle to the lever, F is the force calculated using the Hill equation (Hill, 1938) for each defined interval of jaw closing, and F_{max} is the maximum isometric force of the muscle.

We used a modified version of this equation to consider how *one* muscle can produce a force that acts on *two* levers:

$$F_{act}(A) = \frac{(F_{max} \times F) \times \sin(\vartheta_A)}{\sin(\vartheta_A + \vartheta_B)},$$

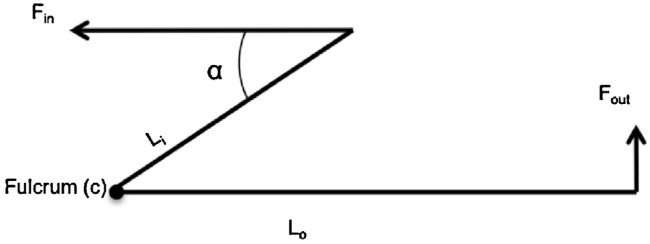
where ϑ is the angle at which the tendon inserts on the lever. This change is important for *C. trichrous* because (see Section 3.2) the AM2 muscle in this species inserts on both the upper jaw (the maxilla) *and* the lower jaw. This mathematical modification enables us to partition the relative force transferred to the upper and the lower jaw by a single muscle during mouth closing.



The standard equation for force produced by a lever is:

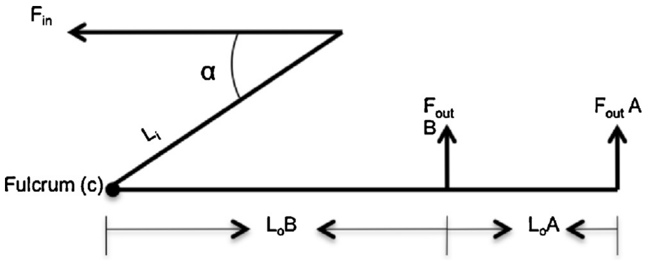
$$F_{out} = F_{act} \times \frac{L_i}{L_o} \times \sin(\alpha),$$

where F_{out} is the force produced by the lever, F_{act} is the force applied by the muscle, L_i is the in-lever distance, L_o is the out-lever distance and α is the angle between the direction of the applied force and the in-lever arm. Angle α changes through jaw closing. This equation works for a simple lever where there is a single force input into the system and a single force output.



However, in *C. trichrous*, because the lower jaw imparts force to upper jaw elements (the maxilla) as well as to the oral teeth of the mandible, forces generated by a single jaw closing muscle are imparted at multiple locations along the out-lever. Thus, we modified the model equations to consider *two* output forces – the maxilla ($F_{out}B$) as well as the oral teeth of the mandible ($F_{out}A$) – both of which are generated through *one* out-lever arm:

(1) $F_{out}B = M_c/((L_oA/L_oB) \times L_oA + L_oB)$ for calculating the force imparted on the maxilla;
(2) $F_{out}A = (L_oA/L_oB)F_{out}B$ for calculating the force imparted on the maxilla to the oral teeth; and
(3) $M_c = F_{act} \times \sin(\alpha) \times L_i$ for calculating the rotational torque of the lever, where α is the angle between the muscle (F_{in}) and the in-lever arm (L_i), and M is the moment or torque about the fulcrum (c).



2.4. Validation of the model

The results of the biomechanical model were compared to empirical values measured from feeding events to ascertain the accuracy of the biomechanical parameters generated. In addition to the assumptions and model parameters described above, the following input parameters were used to assess the model: lower jaw rotation of 10°, upper jaw rotation of 5° (as ascertained from the kinematic data), and a lever displacement of 2 times the displacement of the premaxilla during protrusion. These values fell within the range of parameters for typical feeding behavior of *C. trichrous* feeding on brine shrimp (as measured from the feeding events), thus enabling us to compare model output with the kinematic data to test the ability of the model to predict jaw movements.

Because each lever/muscle attachment to the jaw (AM1 and AM2 for the upper jaw and AM2 and AM3 for the lower jaw) was calculated independently, this methodology generates two independent data series (20 time segments each) of closing times for each jaw (that is, two time series for the upper jaw and two time series for the lower jaw). However, the two muscles that act on each jaw element do not produce distinct movements, so we calculated the mean value of the closing duration using the equations for both jaws to generate an "overall" jaw closing time for each jaw element (that is, one for the upper and one for the lower jaw). Values generated by the models were not statistically different between levers within a jaw (paired *t*-test, $p > 0.05$), which suggests that the various elements of the musculo-skeletal system act simultaneously – a finding that supported the decision to generate overall mean jaw closing times for the upper and lower jaws.

During the process of validating the model, values for the following variables were generated using the model and then compared to empirically collected data from feeding events on brine shrimp: maximum gape, strike velocity, time of gape cycle, time to close lower jaw, time to close upper jaw, and strike distance (see Section 2.2). Mean values were calculated for each variable and paired *t*-tests were used to determine if the model was statistically similar to actual feeding events, under the null hypothesis that the model and actual feeding events are indistinguishable from one another. Three individuals from the kinematic study were used to validate the model in this manner.

2.5. Model output

Force values calculated using our theoretical bite force model, which incorporated the force contribution of the upper jaw, were compared to the original bite force model, which only considered the force produced by the lower jaw. We also noted that, in *Chaetodon* and some other taxa, the lower jaw pushes against the anterior surface of the maxilla, which aids in the closing of the upper jaw (see Section 2.3). Therefore, bite force calculations for the lower jaw made using the original (unmodified) bite force model were compared to the predictions generated by our modified bite force model to assess the force transferred to the lower jaw after the subtraction of the force transferred to the maxilla. Data for three individual *C. trichrous* were entered into both models (equations from Westneat's unmodified bite force model and equations for our modified model) and the output variables were compared using a paired *t*-test.

The modified model was also used to compare feeding behaviors of *C. trichrous* when picking (on hard coral) versus suction feeding (on brine shrimp). Specific kinematic parameters (Table 1) for suction feeding vs. picking were entered into the modified bite force model and used to generate a suite of predictions for the biomechanical outcome for the same individual feeding on two different prey types. Paired *t*-tests were used to determine if the two types of feeding (suction vs. picking) produced model outcomes that were statistically similar to one another, under the null hypothesis that the two behaviors are indistinguishable from one another.

3. Results

3.1. Prey capture kinematics

When feeding, *C. trichrous* individuals gradually approached their prey and then stopped within striking distance. The fish then oriented their bodies toward the prey and protruded the jaws anteriorly in a movement often termed "jaw ram" (sensu: Wainwright and Bellwood, 2002; Liem, 1993), in which the projection of the jaws covers the final distance between predator and prey. Prey were engulfed during the gape cycle and enclosed within the buccal cavity. When *C. trichrous* individuals suction fed in the water column, little movement of the prey occurred until the jaws were almost in direct contact with the prey. At this point, the prey item was rapidly drawn into the buccal cavity, the extended jaws closed on the prey, and the jaws were then adducted. During a picking-based feeding event, the oral jaws also protruded to engulf the prey and closed down on the prey item, which was pulled from the substrate via retraction of the jaws. Thus, a similar suite of behaviors produced both types of feeding events.

However, according to the discriminant function analysis (DFA), individual prey capture events could be placed into their presumed modalities (suction vs. picking) with 100% accuracy. The DFA was also used to evaluate the relative contributions of the kinematic variables in distinguishing strikes on free-floating prey from strikes on benthic attached prey. According to the DFA, magnitude of lower jaw depression, strike velocity, strike time and magnitude of premaxillary protrusion were key to categorizing prey capture events into the two prey capture modes. Thus, the strikes from each feeding mode could be characterized by specific and repeatable differences in the magnitude and timing of body and cranial movements (Table 1). In general, suction-feeding strikes were quite rapid, whereas picking strikes took almost twice as long to complete (0.0096 s versus 0.018 s; Table 1). In addition, picking events were characterized by more than two times greater lower jaw depression (28° vs. 12°; Table 1) and approximately half as much premaxilla protrusion (0.35 cm vs. 0.64 cm; Table 1) relative to suction feeding. However, maximum gape and the change in premaxilla angle were not statistically different between prey capture modes (Table 1 and Fig. 6).

3.2. Myology

The major jaw closing muscle complex, the adductor mandibulae (AM), in *C. trichrous* is composed of three divisions that are responsible for closing the jaws: AM1, AM2 and AM3 (Fig. 7). The AM1 and AM2 originate on the anterior face of the preoperculum and insert on the maxilla through a shared adductor mandibulae tendon (Fig. 7). The outer articulomaxillary ligament connects the maxilla to the mandible and the dorsal fibers of the AM2 also attach to this ligament, which creates a mechanical linkage between the AM2 and the upper and lower jaws. The inner articulomaxillary ligament is connected to the medial face of the maxilla, is fused to the AM2 muscle, and is attached to the AM tendon (Motta, 1982) through an aponeurosis (Fig. 7). This muscle configuration is unusual among teleost fishes (Winterbottom, 1974). In *C. trichrous*, both the AM1 and AM2 are pennate, with an approximate pennation angle of 20°. Based on the orientation of AM1 and AM2, and the results of manual manipulation of the maxilla, it appears that contraction of AM1 and AM2 will generate posterior movement of the ventral aspect of the maxilla, which, in turn, generates an anterio-ventral movement of the tooth-bearing elements of the upper jaw, as well as dorsal movement of the tooth-bearing elements of the lower jaw via the ligamentous connection of the outer articulomaxillary ligament (Fig. 7). In this manner, the contraction of the AM1 and AM2 complex should serve to close the jaws on the prey. The AM3 originates on the anterior face of the preoperculum, medial to the AM2, and inserts on the articular in the same location as the articulomaxillary ligament. The AM1 and AM2 – both of which insert on the maxilla and appear to generate jaw closing – are individually and collectively much larger than the AM3, which inserts only on the lower jaw (AM1 mean mass = 0.011 ± 0.001 g SEM; A2 = 0.0094 ± 0.0007 g SEM; A3 = 0.007 ± 0.001 g SEM; $N = 3$).

3.3. Jaw protrusion mechanism

The functional anatomy of the jaws in *C. trichrous* appears generally consistent with the work of Motta (1982) for *Chaetodon miliaris*; in *C. trichrous*, however, we note several deviations from Motta's mechanism of upper jaw protrusion as proposed for other members of this group. We briefly describe these differences here, as they have direct consequences for jaw kinematics and force production during prey capture in this species. (1) Movement of the nasal bone appears to facilitate upper jaw protrusion. When the

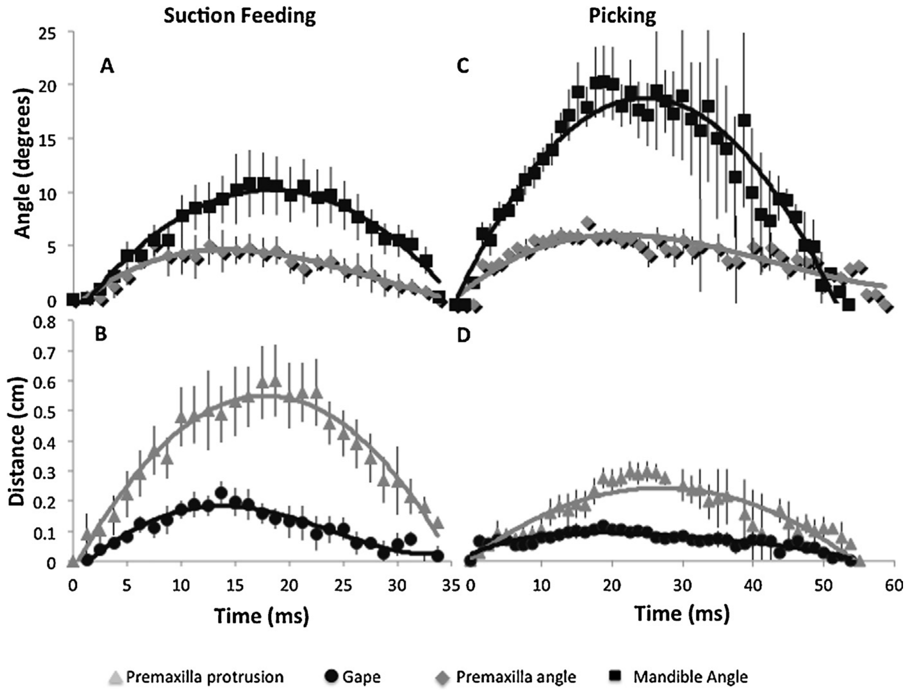


Fig. 6. *Chaetodon trichrous* modulate their prey capture behavior when using (A and B) suction-based feeding in the water column vs. (C and D) picking-based feeding from the substrate. Kinematic variable means ± one standard error of the mean (suction feeding: $N = 5$; picking: $N = 4$) are given here for key kinematic variables, including gape distance (cm), premaxilla protrusion distance (cm), mandible depression angle (°) and premaxilla angle (°). The upper jaw (premaxilla) protrudes farther during suction feeding; in contrast, the lower jaw (or mandible) is depressed to a greater extent during picking.

ventral aspect of the maxilla is pulled anteriorly, the postero-dorsal aspect of the maxilla rotates ventrally, which pulls the nasomaxillary ligament posteriorly and ventrally. This, in turn, pulls on the anterior tip of the nasal bone, forcing the anterior end to rotate ventrally. As the nasal bone pushes down on the ascending process of the premaxilla, the premaxilla is obliged to slide forward – thus facilitating upper jaw protrusion. We note that the anterior end of the nasal bone is dorsal to the ascending process of the premaxilla in *C. trichrous*. In contrast, in many other teleosts the nasal bone is ventral to the premaxilla (Gregory, 1933). (2) Depression

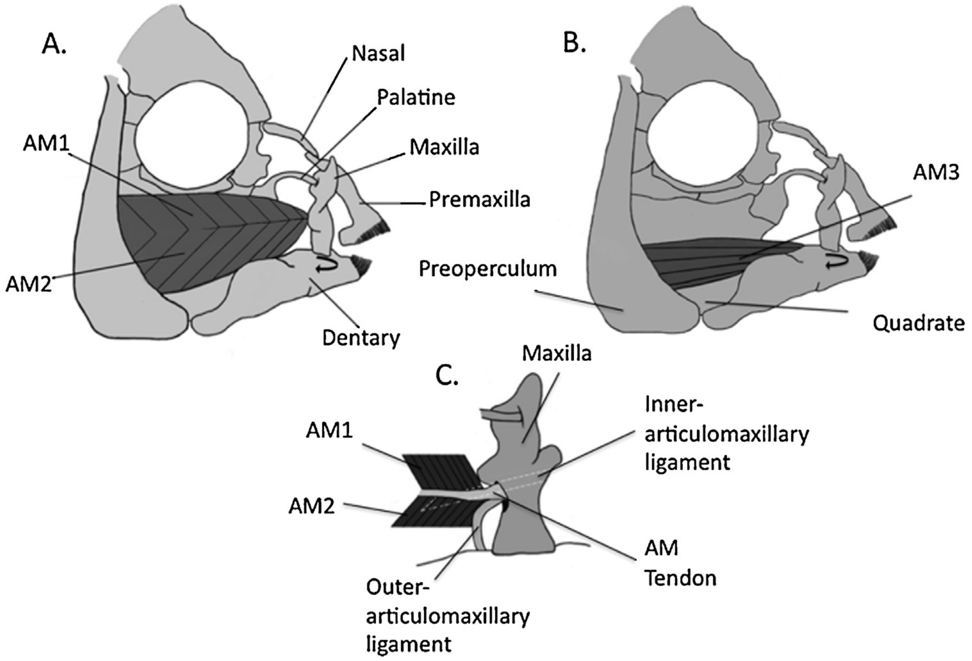


Fig. 7. *Chaetodon trichrous* possess several anatomical features associated with the jaws that appear to deviate from the generalized percomorph bauplan. (A and B) Bones and adductor muscles of the anterior jaws. (A) Two divisions of the adductor mandibulae, AM1 and AM2, insert onto the maxilla via a common tendon. (B) Only one major division of the adductor mandibulae, AM3, inserts directly onto the mandible; here, the superficial muscles (AM1 and AM2) have been removed to reveal AM3. The arrow in (A) and (B) indicates the direction the maxilla twists (long-axis rotation) during mouth opening (maxilla has already twisted in this illustration). (C) The common tendon of AM1 and AM2 attaches to the maxilla (illustrated here before twisting). The outer articulomaxillary ligament attaches the maxilla to the mandible and the AM2 muscle inserts on this ligament. The inner articulomaxillary ligament joins the medial face of the maxilla to the AM2 muscle and AM tendon.

of the mandible causes the maxilla to twist about its longitudinal axis; however, the adductor mandibulae complex pulls the posteroventral aspect of the maxilla posteriorly and does not appear to aid in the twisting movement. In *C. trichrous*, twisting of the maxilla appears to be generated directly by depression of the mandible. Thus, in this species, twisting does not appear to directly cause the premaxilla to protrude. Rather, when the maxilla becomes twisted, there are two functional consequences: (i) the premaxilla/maxilla apposition becomes a rigid connection, which allows little or no dorsal movement of the premaxilla without corresponding anterior rotation of the maxilla – a movement that can be prevented during mouth closing by the contraction of the AM1 and AM2 muscles; (ii) the maxilla "locks" against the premaxilla through the direct alignment of the premaxillary condoyle of the maxilla and the ascending process of the premaxilla. The rotation of the maxilla also moves the lateral and medial connections (i.e., the inner articulomaxillary ligament and the adductor mandibulae tendon) of the AM1 and AM2 muscles on the maxilla into line with the posterior-pivoting axis of the maxilla. This realignment should enable the contraction of the AM muscles to pull the ventral end of the maxilla posteriorly, thus causing the upper jaw to rotate ventrally and closing the mouth. Motta (1982) suggested that, due to the attachments of the AM1 and AM2 to the medial and lateral sides of the maxilla, the maxilla is restrained from rotating about its longitudinal axis. However, this does not appear to be the case for *C. trichrous*. Rather, twisting of the maxilla likely occurs during mouth opening, while the contraction of the AM1 and AM2 (which would be responsible for restraining the maxilla against a twisting movement) must occur during mouth closing. Further, twisting of the maxilla causes ligaments and tendons to reorient in such a way that AM1 and AM2 appear to pull on the adductor mandibulae tendon and the inner articulomaxillary ligament equally, causing the maxilla to rotate posteriorly. (3) The protrusion of the premaxilla in *C. trichrous* appears to be driven by a mechanism other than mandible depression alone because there is an inverse association between mandible depression and premaxilla protrusion – the more the mandible is depressed the less the upper jaw is protruded (Fig. 8).

3.4. Validation of the model

There was no statistical difference between the empirical data collected from feeding events and the timing and displacement predictions made by the model ($n = 3$) for all variables considered here (Table 3). These results suggest that our revised model – which considers upper as well as lower jaw mechanics – accurately predicts the timing and magnitude of movements made during prey capture for this species.

3.5. Jaw forces

A biomechanical model that only considers forces transferred from the jaw-closing muscles to the lower jaw will overestimate lower jaw forces and underestimate upper jaw forces. When the force transferred from the mandible to the maxilla during mouth closing is included in the calculations for the jaws, it greatly reduces the force applied to the prey by the anteriormost teeth of the lower jaw. For example, when the transfer of force to the maxilla is not considered for a suction-feeding fish (Fig. 9), the maximum force output at the tip of the lower jaw is predicted to be 0.051 N (±0.005 SEM), as compared to 0.027 N (±0.003 SEM) when force transfer to the maxilla is taken into consideration ($p < 0.05$). Thus, modeling the lower jaw as a simple lever would overestimate lower jaw bite force production by approximately 50% for a suction-feeding *C. trichrous*. In addition, the upper jaw makes a substantial

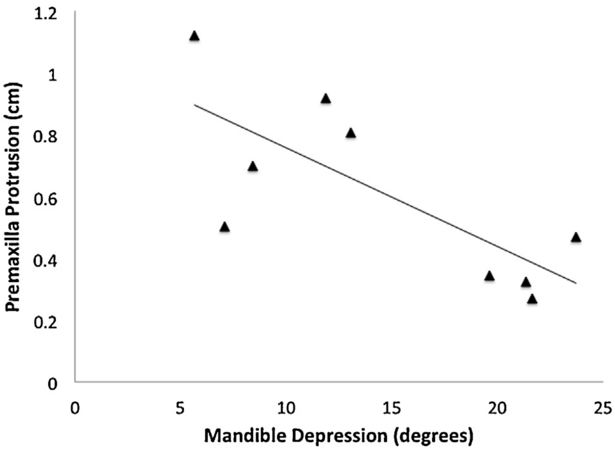


Fig. 8. A complex relationship between mandibular depression and premaxilla protrusion suggests that mandibular depression alone does not drive protrusion of the premaxilla. Protrusion of the premaxilla is negatively associated with lower jaw depression.

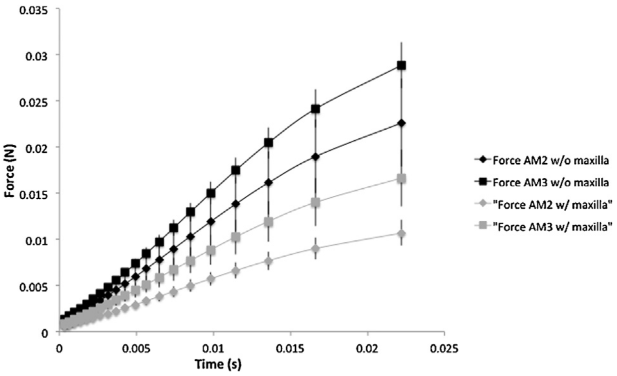


Fig. 9. Force transferred from the lower to the upper jaw results in reduced force at the lower jaw anterior tip during jaw closing as illustrated here by mean ± SEM ($N = 3$) force output of the lower jaw of *Chaetodon trichrous* for the AM2 and AM3 muscles during jaw closing under two modeling scenarios: (i) the output of the model adjusted to include force transfer into the maxilla (gray symbols) and (ii) the output of a common model that does not account for this force transfer (black symbols).

Table 3
Variables used to evaluate the predictive ability of the model generated in the present study. Empirically derived kinematic parameters were compared to those generated by the model ($N = 3$). There was no significant difference between empirical data and model output for any variable considered here ($p < 0.05$).

	Feeding events		Model prediction	
	Mean	SEM±	Mean	SEM±
Maximum gape (cm)	0.1811	0.023	0.1404	0.005
Jaw strike velocity (cm/s)	109.15	16.3	78.31	8.36
Time of gape cycle (s)	0.035	0.005	0.037	0.005
Time to close mandible (s)	0.018	0.0008	0.02	0.004
Time to close premaxilla (s)	0.0079	0.0004	0.0081	0.0005
Strike distance (cm)	1.019	0.05	1.17	0.12

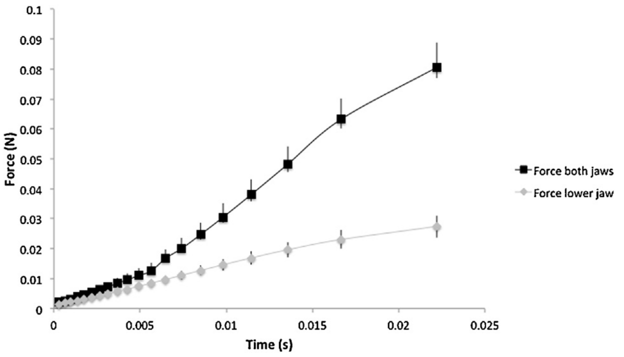


Fig. 10. A model that does not incorporate upper jaw forces will significantly underestimate total bite force in *Chaetodon trichrous*, as illustrated here by mean ± SEM ($N = 3$) total force production during mouth closing at the tip of the lower jaw under two modeling scenarios: (i) a simple model that considers only lower jaw force (gray line and symbols) vs. (ii) a more complex model that considers the force produced by both jaw elements (black lines and symbols). Note that the force contribution of the upper jaw is actually greater than that of the lower jaw; see text for additional details.

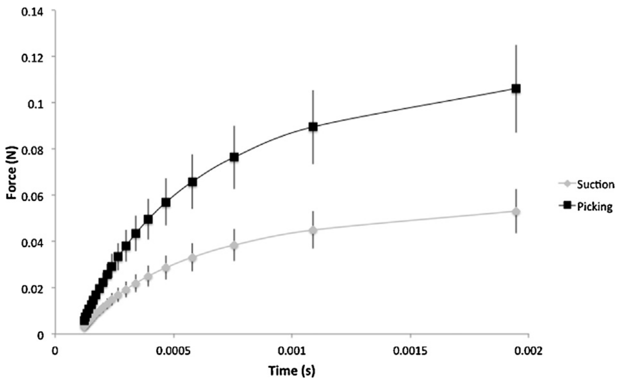


Fig. 11. Modulation of prey capture movements by *Chaetodon trichrous* should produce significantly different jaw forces in different prey capture modes. According to the biomechanical model, mean ± SEM ($N = 3$) force production at the tips of the jaws during suction feeding (gray line and symbols) is less than that produced during picking ($N = 3$) (black line and symbols).

contribution to the overall force produced by the jaws during a feeding event. Using a model that only considers lower jaw forces, the force production of *C. trichrous* is predicted to be 0.027 N; however, when the upper jaw is added to the model, a total force of 0.081 N is anticipated (Fig. 10). In fact, in this system, the upper jaw levers appear to have a greater effective mechanical advantage relative to the lower jaw levers (lower jaw: 0.29 ± 0.01 SEM; upper jaw: 0.38 ± 0.02 SEM; $p < 0.05$).

3.6. *Suction feeding vs. picking*

Variation in magnitude of lower and upper jaw movements across feeding modes has clear consequences for upper and lower jaw bite forces and closing velocities. When comparing suction-based feeding (with 10° lower jaw rotation) with picking-based feeding (20° lower jaw rotation) using the bite force model, it is clear that the degree of mandibular depression directly affects time to jaw closure (Table 4). In addition, relative to suction feeding, it takes approximately twice as long to close the mandible during picking, even though angular velocity of the jaw is approximately 3% greater during the picking behavior. Further, the maximum force the upper jaw can produce is reduced as the premaxilla protrudes farther anteriorly; thus, suction feeding, with 0.6 cm premaxilla protrusion, is less forceful (0.05 N) than picking (0.09 N), which involves 0.3 cm premaxillary protrusion (all values given here are means; cf. Table 4 and Fig. 11).

4. Discussion

4.1. *Upper jaw protrusion mechanism and mechanics*

The head and jaws of *C. trichrous* are a complex arrangement of bones and soft tissues that produce dynamic feeding movements. The adductor mandibulae (AM) complex in this species has undergone anatomical modification that appears to facilitate the modulation of feeding behavior in response to different prey types. The two subdivisions of the AM complex (AM2 and AM3) that attach to the lower jaw at different insertion points may enable these fish to be more forceful *and* have a high jaw-closing velocity (Westneat, 2003; Grubich et al., 2008) because each muscle can be optimized for a single purpose (force vs. velocity). The evolution of this type of closing mechanism may allow the fish to avoid sacrificing one performance parameter to enhance another, as is typically expected in a functional trade-off (e.g., Ferry-Graham and Konow, 2010; Holzman et al., 2011).

The AM complex in *C. trichrous* (and likely in other closely related butterflyfishes) is characterized by anatomical novelties that appear to enhance key aspects of prey capture performance. First, because the AM muscles produce forceful closing movements of both the upper and lower jaws, the total force imposed on the prey is likely greater than could be provided by a single forceful element (Summers, 2000). Second, greater mechanical advantage is generated by the lever systems that underlie the upper jaw – thus increasing overall bite force. Third, because the jaws move toward each other, instead of the lower jaw traveling the entire distance during jaw closing, there is a decrease in the time it takes to close the jaws on an elusive prey item. Finally, the attachment of the AM2 to both the upper and lower jaw elements may be a mechanism to coordinate jaw closing (Hernandez et al., 2009). Two independently controlled elements will facilitate complex jaw movements because one component can move without affecting the other; in contrast, one bifurcated muscle that adducts both elements simultaneously will enable maximal coordination because the movements of the two components are entrained.

Although our model predicts different force values for the lower vs. the upper jaw, this is unlikely to occur. If one jaw element were more forceful, then the weaker element would be pushed away

Table 4
Biomechanical model output generated using parameters taken from suction-feeding events vs. parameters taken from picking events. According to the model, greater lower-jaw depression and reduced upper-jaw protrusion create a slower, more forceful feeding event during picking relative to suction feeding.

	Suction feeding		Picking		*t*-Test
	Mean	SEM±	Mean	SEM±	*p*
Angular velocity AM2 ($^\circ$ s^{-1})	472	43.3	485	45.5	<0.05
Angular velocity AM3 ($^\circ$ s^{-1})	473.1	85.7	491.4	91.6	>0.05
Time to close mandible AM2 (s)	0.022	0.002	0.042	0.004	<0.05
Time to close mandible AM3 (s)	0.023	0.005	0.044	0.009	<0.05
Time to close premaxilla (s)	0.0079	0.0004	0.0081	0.0005	<0.05
Force of upper jaw (N)	0.05	0.006	0.09	0.012	<0.05

when the two jaw elements come together to create a bite – which could reduce bite effectiveness. However, there are several ways to avoid this potential problem. First, the muscles that power movements of the putative weaker element may be operating at more favorable positions on their respective length–tension curves. That is, one or more of the muscular elements adducting the lower jaw could be operating at close to optimal length, while one or more of the muscular elements adducting the upper jaw could be operating on either the ascending or descending limbs of their length–tension curves and producing less-than-maximal force (Gidmark et al., 2013). A possible outcome of this scenario is balanced force production by the two jaw elements during mouth closing. Alternately, the potential problem of asymmetry in upper and lower jaw forces could be ameliorated if force is transmitted from one element to another through connective tissues (Provenzano and Vanderby, 2006). Although modeled here as two components working independently during occlusion, the two jaw elements are physically united by skin and ligaments (Motta, 1982). One ligament of particular interest is the articulodentomaxillary ligament: because it ties the maxilla to the mandible (Motta, 1982), force can be transmitted from the upper to the lower jaw, thus balancing forces across the two elements (for a more extensive discussion of osteichthyan cranial ligaments as a mechanism of force transfer see Westneat, 2004). It is also possible that the smallest division of the adductor mandibulae (A_W), a muscle not included in our model because it is so small, contributes to the force produced by the lower jaw during adduction. However, its very small PCSA makes it unlikely that A_W contributes significant closing forces.

It appears that *C. trichrous* (and perhaps other chaetodontid fishes) have evolved away from a relatively simple form of premaxilla protrusion, where the mandible is depressed, pulling the maxilla anterio-ventrally and propelling the premaxilla away from the neurocranium, to a more complicated mechanism, where protrusion is the result of a suite of bone/muscle/ligament connections that work simultaneously to produce a forceful protrusion that is a key aspect of mouth closing. Although the details of the proposed mechanisms differ, both Alexander (1967) and Motta (1982) suggested that upper jaw protrusion in butterflyfishes is typically generated via the depression (or abduction) of the lower jaw during mouth opening. However, if lower jaw abduction is required to produce upper jaw protrusion, this should generate a positive correlation between upper jaw protrusion and mandible depression – a result that is not seen in this system. The data presented here support the hypothesis that a complex mechanism has evolved to facilitate a form of premaxillary protrusion that actively contributes to jaw closing (see also Konow and Bellwood, 2005).

4.2. *Upper jaw protrusion and picking-based feeding*

Modifications of the jaw apparatus exhibited by *C. trichrous* appear to facilitate picking-based prey capture in several ways. First, the model suggests a ~33% increase in bite force due to forces from the upper jaw, and this increase may improve the ability of a fish to dislodge attached prey from the substrate. Second, the added dexterity of the forceful upper jaw likely enhances the ability of a fish to manipulate the prey during attempts to remove it (Ferry-Graham et al., 2008). Third, because both jaws move toward each other (rather than the lower jaw traversing the entire gape distance to reach a dorsally positioned upper jaw; also see Wilga and Motta, 1998), a mobile premaxilla may increase the probability of capturing elusive prey by decreasing gape closing time. Finally, for fish with mobile upper jaws to have an effective bite, they must develop a mechanism that prevents the upper jaw from being pushed postero-dorsally by the forceful lower jaw during the bite. The added force of the upper jaw may be such a mechanism and it is likely that other teleosts with premaxillary protrusion may possess as-yet-unrecognized mechanisms to restrain the dorsal movements of upper jaw elements during mouth closing.

4.3. *Modulation of feeding behavior*

Individuals of *C. trichrous* alter their feeding behavior when presented with different prey types by varying the movements of the jaws. Suction feeding requires rapid movements, whereas picking is typically characterized by a slower, more forceful bite (Hernandez et al., 2009). During suction-based feeding in *C. trichrous*, the premaxilla extends farther away anteriorly during strike (almost 2 times farther: 7.3% of standard length vs. 4% of standard length) relative to picking-based feeding; this will reduce the force contribution of the upper jaw by reducing jaw mechanical advantage. However, rapid, large-amplitude protrusion of the premaxilla should increase suction production (Carroll et al., 2004), facilitating the capture of midwater prey. Manipulation of prey by the anterior jaws, on the other hand, is facilitated by forcefulness and dexterity (Hernandez et al., 2009). It appears that this species has developed different feeding strategies to circumvent the performance trade-offs often associated with feeding on different prey types.

4.4. *Convergent evolution of a mobile upper jaw*

Upper jaw protrusion is an innovation seen in the most species-rich teleost lineages that may increase the probability of successful prey capture (Staab et al., 2012). Through further modification, forceful, mobile upper jaws may allow these fishes to exploit previously inaccessible prey, such as corals. *C. trichrous* is considered a generalist species that consumes plankton, hard coral and other invertebrates in the wild (Reavis and Copus, 2011). The ability to modulate protrusion to increase suction when midwater feeding and to produce greater force when attempting to remove items from the substrate may increase the success of individuals of *C. trichrous* feeding on a wide range of prey items.

However, within the Chaetodontidae, some species appear to have evolved a more specialized feeding mode that is characterized by elongate jaws. The diet of these species is variable, but often includes both attached invertebrate prey and free-living mobile prey. In species with elongate jaws, the increase in the jaw out-lever should reduce the mechanical advantage of the jaws (assuming muscle properties remain constant), thus reducing jaw force production, which could make the removal of firmly attached prey difficult. We also note that an increase in jaw length should also cause an increase in angular velocity at the tip of the jaws – likely enhancing prey capture success on elusive prey. However, it is also possible that these fishes have altered their muscle architecture (i.e., pennation, mass, etc.) or changed their muscle attachments and lever systems to optimize the operating length of their jaw muscles to counteract the potential loss of bite force.

Other teleost lineages have converged on key morphological and behavioral characteristics with the chaetodontids. Poeciliids and cyprinodontids (Cyprinodontiformes) demonstrate picking-based behavior when procuring food from the water column or from the substrate, as well as a suite of morphological adaptations that facilitate this mode of prey capture behavior (Hernandez et al., 2009). These cyprinodontiform lineages show convergence with the chaetodontids in the following aspects of their functional anatomy: (i) muscle fibers from the AM2 have migrated from the lower jaw to the ligaments that attach to the maxilla. Hernandez et al. (2009) postulated that this architecture produces controlled adduction of the jaws, with both upper and lower jaws acting as third order levers that are simultaneously moved toward one another. (ii) Ligaments connect or 'tie' the premaxilla and maxilla together, which aids in coordinated protrusion of the upper jaw. (iii) The maxilla articulates with the palatine bone via a cartilaginous surface. (iv) A single row of large oral teeth is followed by multiple, posteriorly located rows of smaller teeth. (v) Both groups possess twisting maxillae; interestingly, in both cases the twisting of the maxilla does not appear to contribute to protrusion of the premaxilla. We posit that, in addition to allowing increased dexterity (Hernandez et al., 2009), these morphological modifications provide the ability to modulate the feeding behavior via altered premaxilla protrusion and mandiblular depression to facilitate feeding on a variety of prey types. Thus, it appears that two unrelated teleost lineages, Cyprinodontiformes and Chaetodontidae, have converged on similar morphological feeding adaptations that enhance dexterity for precise picking. In addition, similarities are also seen with the angelfishes (Pomacanthidae) which also feed on benthic attached prey. Similarities between butterflyfishes and angelfishes include multi-tiered arrays of bristle-shaped teeth and a jaw structure where protrusion of the premaxilla aids in closing the mouth (Konow and Bellwood, 2005). We predict that, upon further examination, numerous other teleost fishes will possess analogous evolutionary innovations to facilitate feeding on a diversity of attached prey types.

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