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Feeding performance in Hawaiian stream goby fishes: Morphological and functional analysis

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FEEDING PERFORMANCE IN HAWAIIAN STREAM GOBY FISHES:
MORPHOLOGICAL AND FUNCTIONAL ANALYSIS

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Biological Sciences

by
Takashi Maie
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Accepted by:
Dr. Richard W. Blob, Committee Chair
Dr. Margaret B. Ptacek
Dr. Heiko L. Schoenfuss

ABSTRACT

Distributions of Hawaiian stream fishes are typically interrupted by waterfalls that divide streams into lower and upper segments. Larvae hatched upstream are flushed into the ocean, and must climb these waterfalls to reach adult habitats when returning back to freshwater as part of an amphidromous life cycle. Stream surveys and studies of climbing performance show that *Lentipes concolor* can reach fast-flowing upper stream segments, but that *Awaous guamensis* reaches only slower, lower stream segments. Gut content analyses for these two species indicate that diet differs between them only by 10% or less dry weight for most major components (mostly green algae and invertebrates). This might suggest that feeding kinematics and performance of these two species would be similar. Alternatively, feeding kinematics and performance of these species might be expected to differ in relation to the different flow regimes where they live (faster feeding for *L. concolor*, slower feeding for *A. guamensis*). To test for such differences, we compared suction feeding kinematics and performance between *A. guamensis* and *L. concolor* through analysis of high-speed video footage and geometrical modeling. *L. concolor* showed significantly faster jaw opening performance than *A. guamensis*, which may facilitate suction feeding in the fast stream reaches *L. concolor* typically inhabits. Additionally, performance of jaws during feeding could depend on the proportions and configurations of jaw muscles, like all anatomical lever systems. Differences in feeding behavior and performance among all five native Hawaiian goby fishes (*Sicyopterus stimpsoni*, *Lentipes concolor*, *Awaous guamensis*, *Stenogobius hawaiiensis*, & *Eleotris sandwicensis*) were explored using a mathematical model of

muscle function to provide further ecological and evolutionary insight into their natural history. Simulations of jaw closing indicate that several differences in functional performance correlate well with morphological differences. For example, high output force in adductor mandibulae muscles (*A2* and *A3*) of both *A. guamensis* and *E. sandwicensis* matches expectations from morphology because these muscles are larger in these species than in the other Hawaiian stream gobies. *Stenogobius hawaiiensis* exhibited an alternative morphological strategy for achieving high relative output forces of both muscles, which the placement and configuration of the muscles conveyed high mechanical advantage. The multiple anatomical pathways to similar functional performance in the feeding systems of Hawaiian gobioid fishes reflect a pattern of many-to-one mapping of morphology to performance. In addition, a similar functional differentiation between *A2* and *A3* was evident for all species tested in which *A2* was better suited for forceful movements and *A3* for rapid movements. Thus, diversity of feeding performance of Hawaiian stream gobies does not show simple correlations with their habitats but, rather, seems to reflect a combination of maintenance of functional breadth with retention of some primitive traits, in addition to novel functional capacities in several species.

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CHAPTER ONE

INTRODUCTION

The design of morphological structures can have a major impact on the ability of animals to perform specific functions and, as a result, often correlates strongly with aspects of species ecology (Wainwright and Reilly, 1994). For example, morphological characteristics in fishes often correlate with trophic ecology (Barel, 1983; de Visser and Barel, 1996; Wainwright, 1988; Wainwright and Richard, 1995; Wainwright, 1996; Bouton et al., 1998, 1999, 2002; Osenberg et al., 2004) and spatial distribution (Hugueny and Pouilly, 1999; Bellwood and Wainwright, 2001; Fulton et al., 2001; Wainwright et al., 2002; Bhat, 2005; Ohlberger et al., 2006). Biomechanical studies permit development of hypotheses regarding how, in animals, morphology and patterns of performance are interrelated, and can yield insights into ecological consequences of particular morphological structures (Wainwright et al., 1991). This study attempts to relate morphology of feeding structures to patterns of feeding performance in Hawaiian stream gobies, with the goal of providing ecological (e.g., trophic and spatial) and also evolutionary insight into their natural histories.

The freshwater stream ichthyofauna of the Hawaiian Islands presents an excellent system for evaluating how functional traits of animals relate to their ecology. Hawaiian freshwater streams have an ichthyofauna that consists of five amphidromous goby species: *Sicyopterus stimpsoni* Gill (family Gobiidae), *Lentipes concolor* Gill (family Gobiidae), *Awaous guamensis* Valenciennes (family Gobiidae), *Stenogobius hawaiiensis* Watson (family Gobiidae), and *Eleotris sandwicensis* Vaillant and Sauvage (family

Eleotridae) (Fitzsimons et al., 1993). The streams that these fishes inhabit are typically interrupted by waterfalls, dividing the streams into lower and upper reaches (Schoenfuss and Blob, 2003). Like other amphidromous goby species in the Indo-Pacific and Caribbean (Manacop, 1953; Fukui, 1979; Sakai and Nakamura, 1979; Harrison, 1993; Parenti and Maciolek, 1993; Bell, 1994; Berrebi et al., 2005), newly hatched larvae are swept by flowing water downstream into the ocean, where they develop for several months (Radtke et al., 1988) as part of the oceanic zooplankton before migrating back to adult habitats in freshwater (Keith, 2003; McDowall, 2003, 2004). Adults of three species of Hawaiian stream gobies (*S. stimpsoni*, *L. concolor*, and *A. guamensis*) live above waterfalls, and their larvae must climb waterfalls, often tens of meters or more in height, to reach adult habitats during their amphidromous life cycle. The ability to climb develops after a post-larval metamorphosis (Nishimoto and Fitzsimons, 1999; Schoenfuss and Blob, 2003; Blob et al., 2006) and is facilitated by fusion of a pair of pelvic fins into a ventral adhesive disc or pelvic sucker (Fukui, 1979; Sakai and Nakamura, 1979; Bell, 1994; Fitzsimons and Nishimoto, 1995), which allows these fish to resist both gravitational and hydrodynamic (i.e., drag) forces during vertical climbing. In contrast, the two remaining species cannot climb and are confined to the lower stream reaches, returning to these lower reaches upon re-entering freshwater. These are *E. sandwicensis*, a piscivorous and ambush type predator, and *S. hawaiiensis*, a detritivore that lives on sandy stream bottoms. The pelvic sucker is lacking in *E. sandwicensis* (pelvic fins remain separated) and weak in *S. hawaiiensis*. In addition to these distinctions between non-climbing and climbing species, climbing species also exhibit differences in climbing

style (i.e., “inching” of *S. stimpsoni* vs. “powerburst” of *L. concolor* and *A. guamensis*) and performance (i.e., climbing bout duration, climbing speed, and % time of being in motion) (Blob et al., 2006). Blob et al. (2006) correlated these differences in climbing performance with differences in habitat distribution. Although both adult and juvenile *A. guamensis* can be found in lower stream reaches, the only *L. concolor* found in the lower reaches are juveniles migrating upstream, and adult *L. concolor* penetrate much further upstream than adult *A. guamensis* (Tate, 1997; Blob et al., 2006). Faster climbing by juvenile *L. concolor* may explain their ability to surmount major waterfalls (e.g., more than 120 m of Akaka Falls, Hawai’i: Yamamoto and Tagawa, 2000) and penetrate further upstream than juvenile *A. guamensis* (Blob et al., 2006).

Differences in locomotor kinematics and performance among fishes are often correlated with differences in locomotor morphology, and can help to determine differences in spatial ecology among species (Bellwood and Wainwright, 2001; Fulton et al., 2001; Wainwright et al., 2002). However, differences in climbing performance may not fully explain the difference in distribution of Hawaiian waterfall-climbing gobies throughout their freshwater habitats. For instance, as Blob et al. (2006) pointed out, differences in climbing performance of *L. concolor* and *A. guamensis* did not predict complete dissociation of adult habitats between the two species.

In addition to locomotor capacity, dietary data (including substantial overlaps) for Hawaiian stream gobies, provide an important context for this study. For instance, *E. sandwicensis* feeds on mostly animal foods (56.2% dry biomass of gut content: Kido, 1996), consisting of arthropods, insects, and other animal materials that include incoming

gobioid larvae (Tate, 1997). Some plant materials including Chlorophyta (green algae) especially *Cladophora* sp. (e.g., 28.7% dry weight: Kido, 1996) also have been recovered from *E. sandwicensis* gut contents, but the extent to which these are digested, or may have been consumed incidental to the capture of animal prey, is not clear (M. Julius, personal communication). In contrast, *L. concolor* seems to consume a greater proportion of plant materials (93.1% dry biomass), mostly *Cladophora* sp. (green-algae), and a smaller proportion of animal material (6.5% dry biomass). *Stenogobius hawaiiensis* shows patterns similar to those of *L. concolor*. *Sicyopterus stimpsoni* and *A. guamensis* have shown significant differences in the use of food resources (prey type). The diet of *S. stimpsoni* consists of 22.6% blue-green algae and 54.2% of diatoms, whereas that of *A. guamensis* shows 43.0% of green-algae (Kido, 1997). Dietary differences between *S. stimpsoni* and *A. guamensis* may help them to coexist in the same habitat (Kido, 1997). Interestingly, dietary patterns of *L. concolor* and *A. guamensis* substantially overlap, such that their diets differ by only 10% or less dry weight for most major components, which include mostly green-algae, *Cladophora* sp., and small invertebrates. This may be a driving factor in the disassociation of their habitats (Kido, 1996, 1997).

The primary purpose of this study is to evaluate the feeding performance of Hawaiian stream gobies as a factor that potentially affects their trophic ecology (resource use) and spatial ecology (habitat distribution). Although dietary competition has been proposed between *L. concolor* and *A. guamensis*, differences in feeding mechanics and performance have not been evaluated between these species, or for any other goby. One

biomechanical aspect of function that contributes to feeding performance is the kinematics of feeding structures during prey capture (suction feeding). A particular pattern of jaw movements may be more effective than others under certain environmental conditions (e.g. water flow velocities) and, therefore, might be predicted for species living in these conditions if feeding performance is to be maximized.

Importantly, the mechanics of jaw movement in fishes are closely correlated to the morphology and functional design of the feeding apparatus and other cranial structures, which can influence feeding performance and, thus, resource use (Wainwright, 1996; Westneat, 2003). In particular, the lever system of the mandible can determine the force and speed of mandibular movements, and has been extensively studied in many teleostean systems as an indicator of feeding performance (Richard and Wainwright, 1995; Wainwright and Shaw, 1999; Cutwa and Turingan, 2000; Westneat, 2003; Van Wassenbergh et al., 2005). In anatomical lever systems, including those in biological systems such as the limb and jaw skeletons of vertebrates, the ratio of in-lever arm to out-lever arm (i.e., mechanical advantage) determines how high an output force can be generated relative to the input force. Conversely, the velocity advantage is the ratio of out-lever arm to in-lever arm (i.e., inverse of mechanical advantage), and it determines how fast an output velocity of lever motion would be generated relative to the input velocity in a system. The inverse relationship between the mechanical advantage and velocity advantage of lever systems represents a trade-off between force and speed of movement in musculoskeletal systems, such as those of the jaws. In vertebrate feeding systems, the greater the mechanical advantage a jaw has, making it capable of

transmitting greater force, the lesser the velocity advantage it can have, causing it to move more slowly. These mechanical relationships can help to indicate relationships between the performance and biological role of feeding structures. For example, species that capture prey by biting may have a greater mechanical advantage (i.e., short and stout jaws with out-lever shortened and, thus, out-put force enhanced), and species that obtain food by suction feeding may, in turn, have a lesser mechanical advantage, or conversely greater velocity advantage because of elongated and gracile jaws with out-lever lengthened and, thus, out-put velocity enhanced (Barel, 1983; Wainwright and Richard, 1995). In the context of previous studies that have shown strong correlations between morphology and feeding performance in teleosts (Barel, 1983; Westneat, 1990, 1995; Wainwright and Shaw, 1999; Westneat, 2003), I attempt to examine the jaw lever system of Hawaiian stream gobies as an anatomical model for predictions about specific aspects of feeding performance in these species (i.e., jaw closing). I also directly evaluate other aspects of feeding performance through direct measurements of feeding kinematics. Although cases have been documented in which changes in feeding ability are attributed to changes in muscle activation patterns through evolution, neuromuscular patterns tend to be conserved in many feeding modes of teleosts (Lauder, 1983; Wainwright and Lauder, 1986; Wainwright, 1989; 1996; Friel and Wainwright, 1998; Alfaro et al., 2001; Wainwright, 2002). Fish taxa examined in this study are also relatively closely related to each other (Parenti and Thomas, 1998; Thacker, 2003), making the conservation of neuromuscular patterns for prey capture more likely. Therefore, musculoskeletal morphology and kinematics of the jaws as a basis for understanding variations in feeding

ability are compared and evaluated. In addition to providing insight into the relationship between morphology and ecology in these species, this work is the first examination of feeding mechanics and performance in the order Gobioidae, one of the most speciose teleostean groups with more than 2000 species in 268 genera worldwide (Nelson, 1994; Thacker, 2003).

Through functional studies (see Chapter 2 and Chapter 3), which evaluate and compare feeding performance of the five native species of Hawaiian stream gobies (*S. stimpsoni*, *L. concolor*, *A. guamensis*, *S. hawaiiensis*, and *E. sandwicensis*), I believe that this study improves understanding of how a current mosaic of ichthyofauna in freshwater streams of Hawaiian Islands is being shaped.

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CHAPTER TWO

FEEDING KINEMATICS AND PERFORMANCE OF HAWAIIAN STREAM GOBIES, *LENTIPES CONCOLOR* AND *AWAOUS GUAMENSIS*: LINKAGE OF FUNCTIONAL MORPHOLOGY AND ECOLOGY

Introduction

The freshwater ichthyofauna of the Hawaiian Islands provides a novel system for evaluating how functional traits of animals correlate with their ecology, because streams on the Hawaiian Islands present distinctive environmental challenges for fishes that inhabit them. Hawaiian streams are typically characterized by steep gradients and high velocity water flow, strong flash floods after heavy rain falls or hurricanes, and segmentation into upstream and downstream reaches by waterfalls that can be tens of meters tall (Fitzsimons and Nishimoto, 1995). The native ichthyofauna of these streams consists of five gobioid species, four from the family Gobiidae and one from the family Eleotridae (Fitzsimons et al., 1993), that share an amphidromous life history that helps them to maintain populations in these challenging habitats (Ford and Kinzie, 1982; Tate et al., 1992; Fitzsimons and Nishimoto, 1996). Like other amphidromous goby species (Manacop, 1953; Fukui, 1979; Sakai and Nakamura, 1979; Harrison, 1993; Parenti and Maciolek, 1993; Bell, 1994; Berrebi et al., 2005), newly hatched larvae of Hawaiian stream gobies are swept by stream currents out to the ocean, where they develop for several months in the ocean before migrating back to freshwater habitats (Keith, 2003; McDowall, 2003, 2004). Waterfalls present a substantial challenge to the penetration of upstream habitats by returning juveniles, but some species have evolved novel structures and functional capacities that allow them to climb up these obstacles (Blob et al., 2006).

In the Hawaiian Islands, juveniles of two species, *Lentipes concolor* and *Awaous guamensis*, climb using a “powerburst” mechanism, in which fish push off against the substrate with their pectoral fins and move upwards using several cycles of axial undulation before reattaching to the substrate with a sucker formed by fusion of the pelvic fins (Fitzsimons and Nishimoto, 1990; Schoenfuss and Blob, 2003). The distribution of species in the streams correlates with their ability to climb (Blob et al., 2006). *Awaous guamensis* juveniles are slow climbers and adults are unable to climb, whereas in *L. concolor* juveniles are rapid climbers and adults retain climbing ability (Blob et al., in press). Correspondingly, *A. guamensis* typically are restricted to lower stream reaches, whereas *L. concolor* live in upper stream reaches beyond the penetration of *A. guamensis* (Kinzie, 1988; Brasher, 1996; Tate, 1997; Blob et al., 2006).

These studies of locomotor function and ecology in climbing gobies provide a context for examining the performance of other functional systems to evaluate how they contribute to the survival of these species in their respective environments. One of the most important functional systems affecting the survival of animals besides locomotion is feeding, which allows prey capture and, thus, energy acquisition for survival and reproductive success. Three primary modes of prey capture have been described for teleost fishes (Liem, 1980; Lauder, 1983): (1) ram feeding, in which movement of the body of a fish overtakes a mass of water and prey item; (2) suction feeding, in which a subambient pressure gradient created by expansion of the volume inside the buccal cavity draws a mass of water and prey item into the mouth; and (3) manipulation, in which the jaws are used to either bite prey or scrape it off of the substrate (i.e., by means of direct

contact to either prey or substrate). The two powerburst climbing species, *L. concolor* and *A. guamensis*, both make extensive use of suction feeding and seem to have very similar diets. According to gut content analyses by Kido (1996), dry weights of most major diet components differ by less than 10% between these two species, and include several varieties of green algae and small invertebrates. Because of this similarity in their diets, the feeding performance of these species might also be expected to be similar (e.g., character convergence: Vadas, 1990). However, habitat differences in water flow velocity could potentially lead to differences in feeding performance between these species. In particular, preliminary observations (Schoenfuss and Blob, 2007) suggested that the jaw lever system of *L. concolor* would be better suited for fast movements than that of *A. guamensis*. Because *L. concolor* live in upper stream reaches where water flow is typically faster (Schoenfuss and Blob, 2007) and are often observed swimming into the fast flow of the water column during feeding rather than staying in slower flow at the stream bottom (personal observation), it might be advantageous for *L. concolor* to be able to feed more quickly than *A. guamensis* in order to capture prey that might otherwise drift away.

To test the hypothesis that habitat differences are correlated with feeding performance differences in Hawaiian stream gobies, we examine morphology, kinematics, and performance of the feeding system in the powerburst climbing species, *L. concolor* and *A. guamensis*. We predict that the species that typically lives in faster flowing water (*L. concolor*) will show faster feeding performance relative to *A. guamensis* that will be correspond with the difference in habitat between these species.

Materials and Methods

Specimen acquisition and morphological comparisons

Specimens of both *L. concolor* and *A. guamensis* were captured (Clemson AUP# 40061 and 50089) while snorkeling using an o'pae net (a fine, spherically shaped mesh with a narrow opening at the top of a bowl shaped basket). Collections were made during three field seasons (2004-2006) from their native stream habitats. Specimens of *L. concolor* ($N = 29$) were collected in Hakalau, Nanue, Manoloa, and Kamae'e streams above waterfalls on the Island of Hawai'i, and in upper reaches of Hanakapi'ai stream on the Island of Kaua'i. Specimens of *A. guamensis* ($N = 46$) were collected in Wailoa Pond and the lower stream reaches of Hakalau and Nanue streams on the Island of Hawai'i, and in the lower stream reaches of Hanakapi'ai and Limahuli streams on the Island of Kaua'i. Specimens were preserved in 70% ethanol, after which jaw muscles and skeleton were dissected under a dissecting scope (Nikon SMZ 1000) and photographed using a digital camera (Nikon CoolPix 4300) prior to measurement. For each specimen, in-lever arms and out-lever arms for both jaw opening and closing were measured from digital photographs using NIH Image software for Apple Macintosh, developed by the U.S. National Institutes of Health and available on the web at <http://rsb.info.nih.gov/nih-image/>. Lever arm ratios (in-lever: out-lever) for jaw closing and opening were calculated from these measurements. For jaw opening, the in-lever arm is the distance between the quadratomandibular joint and the caudoventral point of the dentary, on which the interoperculomandibular ligament inserts; the out-lever arm is the distance between the quadratomandibular joint and the anterior tip of the dentary (Figure 2.1).

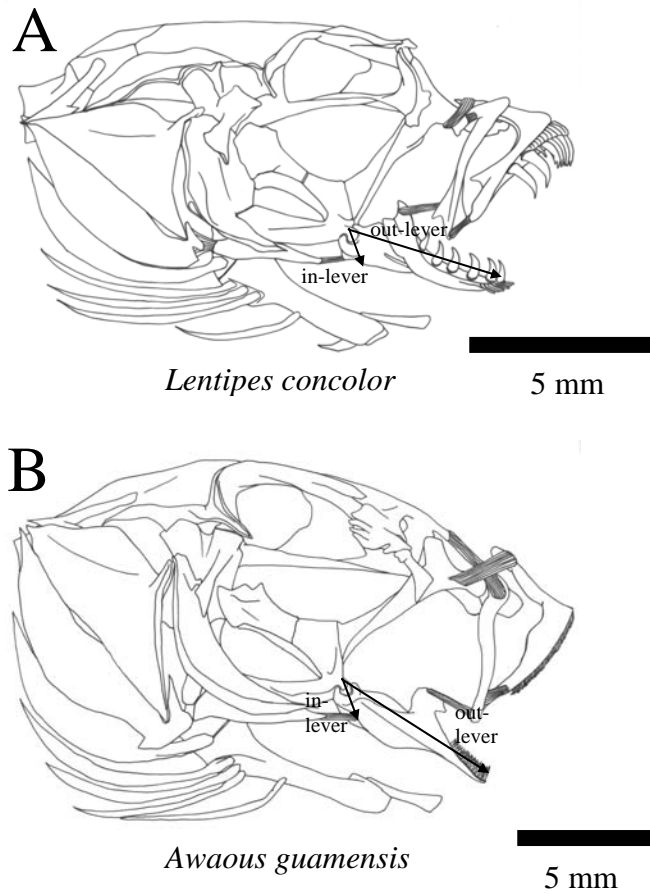


Figure 2.1: In-lever arm and out-lever arm for jaw opening on drawings of cranial skeleton of *Lentipes concolor* (A) and *Awaous guamensis* (B). Note: scale bars indicate 5 mm.

For jaw closing, the in-lever arm is the distance between the quadratomandibular joint and the superior tip of the coronoid process of the dentary, and the out-lever arm is the same as for jaw opening (Westneat, 2003). In the mechanical relationships of lever systems, lower ratios of in-lever arm to out-lever arm provide a greater “velocity advantage” (Westneat, 1994; Wainwright and Richard, 1995), facilitating faster jaw movement. The significance of differences in lever ratios between the two species and between sexes within each species were evaluated using t-tests.

Kinematic analysis

In the 2005 and 2006 field seasons, prior to dissections and morphological measurements, kinematics of suction feeding were filmed for a total of three individuals each of *L. concolor* (3 males, 83.9 mm, 91.7 mm, and 95.0 mm total length) and *A. guamensis* (2 females, 68.6 mm and 102.7 mm total length; 1 male, 122.2 mm total length). For both species, males may grow to larger maximum body length than females (Maciolek, 1977; Ha and Kinzie, 1996), however, especially for *A. guamensis*, medium sized individuals appear not to differ in body length between sexes (personal observation). Animals used for filming were from Hakalau, Manoloa, and Kamae'e streams (*L. concolor*) and Hakalau stream and Wailoa Pond (*A. guamensis*), all from the Island of Hawai'i. Gobies captured for filming were separated individually into 37.9 liter aquaria filled with aerated stream water at ambient temperature (~19°C), and housed at a research facility of the Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources (DAR). Fish were acclimated for three days prior to the beginning of filming. During both acclimation and filming periods, fish were fed with commercially available brine shrimp (*Artemia* sp.), as it was the only readily available prey item that could elicit feeding strikes by both species at a specified tank location, allowing repeated filming of behaviors. Brine shrimp were loaded into transparent air stone tubing (3 mm hollow diameter), for which one end was submerged and the other was held outside the tank. The food was released in front of each fish using a rubber bulb attached to the end of the feeding tube outside the tank.

To evaluate details of feeding kinematics for *L. concolor* and *A. guamensis*, digitally synchronized lateral and ventral views of feeding strikes were filmed at 500 frames/sec using two Phantom V4.1 high-speed digital cameras. Ventral views were obtained using a mirror placed under each aquarium angled 45° relative to the transparent floor of each tank. All sequences were filmed in still water in the tanks where fish were housed, minimizing stress that could be imposed by transferring fish between tanks.

High-speed video sequences of feeding were saved as AVI files, and the positions of landmarks on the heads of the fishes were digitized for every other frame using a modification of the public domain NIH Image software for Apple Macintosh (the modification, QuickImage, was developed by J. Walker and is available at <http://usm.maine.edu/~walker/software.html>). For both species, 11 landmark points in lateral view and 8 points in ventral view were digitized. The 11 points in lateral view included the anterior tip of the premaxilla, anterior tip of the mandible, ventral border of the hyoid arch, center of the eye, anterior tip of the neurocranium (joint between maxilla and neurocranium), top of the neurocranium (insertion point for the epaxial muscle), posterior tip of the operculum, front edge of the food item, dorsal tip of the pectoral fin base, and ventral tip of the pectoral fin base (Figure 2.2). The eight points in ventral view included the anterior tip of the premaxilla, anterior tip of the mandible, a point on the posterior border of the hyoid arch, lateral tips of the premaxilla (right and left), lateral tips of the operculum (right and left), and front edge of the food item (Figure 2.2).

Custom programs written in Matlab 5.0 (Mathworks, Inc.; Natick, MA, USA) were used to calculate kinematic variables for every frame of digitized coordinate data,

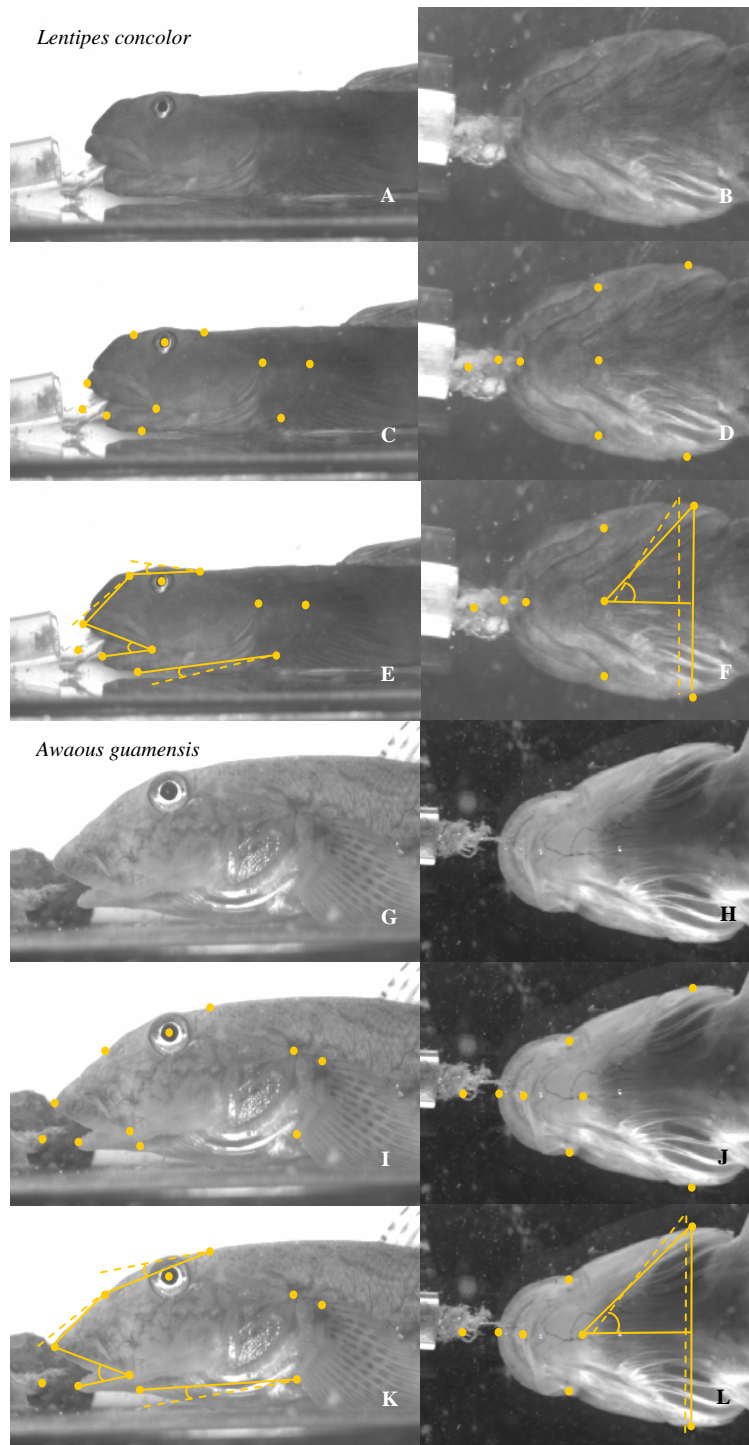


Figure 2.2: Video still images of feeding behaviors of *Lentipes concolor* and *Awaous guamensis* with 11 lateral landmarks on the head (C and I) and 8 ventral landmarks on the head (D and J) and angles between vectors formed by landmark points (E, F, K, and L).

including the linear and angular displacements of the upper and lower jaw, neurocranium, hyoid, and opercula, as well as maxima of these displacements and timing variables associated with movement of feeding apparatus. After evaluating these parameters, QuickSAND software (Walker, 1998; available at <http://www.usm.maine.edu/~walker/software.html>) was used to fit a quintic spline to the kinematic calculations for each feeding strike, smoothing the data and normalizing all strikes to the same duration in order to obtain mean kinematic profiles for each variable. Sixteen focal kinematic variables were calculated: (1) maximum gape angle, the maximum angle between upper and lower jaws; (2) time to maximum gape angle, time from the beginning of feeding strike (i.e., first jaw movement) to the maximum gape; (3) maximum mandibular depression angle, the maximum angle between the position of the mandible at the beginning of feeding strike and the position of the mandible at maximum gape; (4) time to maximum mandibular depression angle, time from the beginning of the feeding strike to the maximum mandibular depression; (5) maximum upper jaw protrusion, the maximum displacement of the upper jaw (premaxilla); (6) time to maximum upper jaw protrusion, time from the beginning of the feeding strike to the maximum upper jaw protrusion; (7) gape cycle, time between the beginning of feeding strike and the end of the strike; (8) time to jaw closure from the maximum gape, time from the maximum gape to the end of the feeding strike (9) maximum cranial elevation angle, the maximum angle between the initial position of a vector, formed by the anterior tip of the neurocranium and the top of the neurocranium at the beginning of feeding strike, and the position of the same vector at maximum cranial elevation; (10) time to

maximum cranial elevation, time from the beginning of the feeding strike to the maximum cranial elevation; (11) maximum hyoid depression angle, the maximum angle between the position of a vector, formed by a point at the ventral border of the hyoid arch and a point at the ventral tip of the pectoral fin base, at the beginning of feeding strike, and the position of the same vector at maximum hyoid depression; (12) time to maximum hyoid depression angle, time from the beginning of the feeding strike to the maximum hyoid depression; (13) maximum hyoid retraction angle, the maximum angle between the long axis of the head and the ceratohyal on right side at the hyoid arch; (14) time to maximum hyoid retraction angle, time from the beginning of the feeding strike to the maximum hyoid retraction angle; (15) maximum opercular expansion, the maximum distance between the lateral tips of the two opercula; (16) time to maximum opercular expansion, time from the beginning of the feeding strike to the maximum opercular expansion. Variables were calculated separately from either lateral or ventral views, as appropriate, and represent two dimensional projections of three dimensional angles (Van Wassenbergh et al., 2005). The significance of differences in kinematic and performance variables between species were evaluated using Mann-Whitney *U*-tests. A total of 35 feeding trials from three individuals of *L. concolor* (10, 14, and 11 sequences from each individual) and 28 trials from three individuals of *A. guamensis* (8, 8, and 12 sequences from each individual) were analyzed in this study.

In addition to kinematic variables, one of the most important aspects of feeding performance to ensure success of prey capture is the speed at which buccal volume is increased. Generating faster movements in elements of the feeding apparatus can

increase the speed of water entering the buccal cavity (Osse, 1969; Muller and Osse, 1984; Wilga and Motta, 2000), thereby maximizing suction pressure (Osse, 1969; Sanford and Wainwright, 2002; Svanback et al., 2002). Although buccal pressure could not be directly measured in our study, the suction pressure generated by expansion of the buccal cavity during a feeding strike could be estimated by modeling changes in the volume of the buccal cavity through the time course of feeding strikes, an approach used previously in studies of other actinopterygian fishes (Barel, 1983; Liem, 1990). The pressure differential leading to suction can be calculated using Bernoulli's theorem of constancy of the sum of dynamic and static pressures for water flowing into the mouth as:

$$(P_0/\rho g) - (P_1/\rho g) = (1/2)(v^2)/g \quad \text{Eq. 1}$$

where P_0 is the pressure in the surrounding water, P_1 is the pressure inside the buccal cavity near the mouth, v is the speed of flowing water, ρ is the density of water (1,000 kg/m³ for freshwater: Vogel, 2003), and g is gravitational acceleration (Osse, 1969; Alexander, 1983). The speed of water flowing into the mouth can be obtained by calculating the change in volume of the buccal cavity during the time to reach maximum buccal expansion (i.e., the time to maximum gape) over the surface area of the mouth orifice as:

$$\text{Speed of flow } (v) = (dV/dt)/(Area_{ORIFICE}) = (\Delta V/T_G)/(\pi R_G^2/4) \quad \text{Eq. 2}$$

where ΔV is the buccal volume change, T_G is the time of gape change, and R_G is the gape, which serves as a diameter for calculation of the area. Considering highly kinetic elements of the teleostean cranium, buccal volume was estimated geometrically by modeling the cavity (Barel, 1983; Liem, 1990) as a pair of conical frusta dividing the cavity into two compartments (i.e., an anterior cavity formed by the upper and lower jaw and a posterior cavity formed by the opercular region of the cavity) as:

$$V = (L_{Ant}/3)(A_1 + A_2 + (A_1 A_2)^{1/2}) + (L_{Post}/3)(A_2 + A_3 + (A_2 A_3)^{1/2}) \quad \text{Eq. 3}$$

where V is the buccal volume, L_{Ant} is the height of the anterior conical frustum, A_1 is the area of opening of the mouth, A_2 is the area of opening at the eye-hyoid arch region, L_{Post} is the height of the posterior conical frustum, and A_3 is the area of the opening of opercular region where the maximum displacement of the operculum occurs. In addition, the Hagen-Poiseuille equation was used in further assessment of suction performance as:

$$\Delta P = (8\nu\rho L)/(\pi R^4) \quad \text{Eq. 4}$$

where ΔP is the pressure differential, ν is the rate of water flow, ρ is the density of water (i.e., freshwater), L is the length of the tube (i.e., distance from mouth to opercula), and R is the radius of the tube. This relationship indicates that an increased rate of water flow, an increased length of the tube, and a decreased area of the opening of the mouth can

maximize pressure differential and, thus, performance in suction feeding (Alexander, 1967, 1983; Osse, 1969; Pietsch, 1978).

Results

Morphology of the feeding apparatus

No significant differences were found between males and females of either species in either jaw opening or closing lever ratios (Table 2.1). This similarity between the sexes allowed measurements from both sexes to be pooled in comparisons between the species. Comparing these pooled samples, the mean lever ratio for jaw opening is about 10% smaller in *L. concolor* than in *A. guamensis* (0.136 vs. 0.149, respectively: Table 1), indicating a greater velocity advantage for *L. concolor* during jaw opening. Although a t-test on lever ratios did not indicate a significant difference between the species at $P < 0.05$, there appears to be a trend that the difference between the species was consistent with the potential for *L. concolor* to have faster jaw opening in its feeding strike than *A. guamensis* ($P = 0.0998$: Table 2.1). For the jaw closing lever, differences between *L. concolor* and *A. guamensis* are less substantial ($P = 0.1393$: Table 2.1).

Lever Ratio	Jaw open	<i>P</i> value
<i>L. concolor</i> , f	0.148 ± 0.024	
<i>L. concolor</i> , m	0.133 ± 0.028	0.2765
<i>A. guamensis</i> , f	0.154 ± 0.028	
<i>A. guamensis</i> , m	0.146 ± 0.040	0.4982
<i>L. concolor</i> , pooled	0.136 ± 0.027	
<i>A. guamensis</i> , pooled	0.149 ± 0.036	0.0998

Lever Ratio	Jaw close	<i>P</i> value
<i>L. concolor</i> , f	0.416 ± 0.037	
<i>L. concolor</i> , m	0.430 ± 0.055	0.5750
<i>A. guamensis</i> , f	0.422 ± 0.043	
<i>A. guamensis</i> , m	0.403 ± 0.050	0.2072
<i>L. concolor</i> , pooled	0.428 ± 0.052	
<i>A. guamensis</i> , pooled	0.410 ± 0.048	0.1393

Table 2.1: Lever ratios for jaw opening and closing for female, male, and pooled samples of *L. concolor* and *A. guamensis*. Values are means ± standard deviation.

Feeding kinematics and performance

Although both species fed in a benthic setting during trials, none of the head movements of either species was interrupted by the floor of the filming arena because the pelvic sucker served as a platform that gave space to the moving elements, especially the mandible and hyoid. Both species demonstrated general kinematic patterns similar to those exhibited by a wide range of actinopterygian fishes (Osse, 1969; Lauder, 1980; Lauder and Liem, 1981; Ferry-Graham and Lauder, 2001; Grubich, 2001). Concomitant with maximum gape, maxima of mandibular depression and cranial elevation occurred (Figure 2.3). Slightly later in the gape cycle, maxima of premaxillary protrusion, hyoid depression and retraction, and opercular expansion almost simultaneously followed (Figures 2.3, 2.4). Some kinematic elements were held in position for a prolonged period (i.e., premaxillary protrusion, cranial elevation, hyoid depression, and opercular

expansion) after reaching each of their maximum values (Figures 2.3, 2.4). Although both species showed slight forward movement of the entire body during each feeding strike, there was no evidence of gill opening during expansive and compressive phases of all strikes that we filmed indicating food was acquired primarily through suction, rather than ram feeding.

Lentipes concolor showed greater and faster movements of the feeding apparatus during feeding strikes than *Awaous guamensis* (Table 2.2 and Figures 2.3, 2.4).

Variable	<i>L. concolor</i>	<i>A. guamensis</i>	<i>P</i> value
Maximum gape angle (°)	43.8 ± 13.7	32.5 ± 16.0	0.0003***
Time to maximum gape angle (ms)	26.1 ± 12.7	54.4 ± 27.2	<0.0001***
Maximum mandibular depression angle (°)	37.1 ± 9.8	24.9 ± 14.6	<0.0001***
Time to maximum mandibular depression angle (ms)	31.5 ± 13.4	61.3 ± 27.4	<0.0001***
Maximum upper jaw protrusion (mm)	2.1 ± 0.6	1.5 ± 0.5	<0.0001***
Maximum upper jaw protrusion (BL)	0.023 ± 0.006	0.016 ± 0.006	<0.0001***
Time to maximum upper jaw protrusion (ms)	51.6 ± 21.3	80.9 ± 30.7	<0.0001***
Gape cycle (ms)	77.7 ± 26.8	106.8 ± 31.5	0.0005**
Time to jaw closure from maximum gape (ms)	51.6 ± 20.9	52.4 ± 15.5	0.8572
Maximum cranial elevation angle (°)	7.1 ± 3.3	3.1 ± 2.3	<0.0001***
Time to maximum cranial elevation angle (ms)	47.0 ± 24.0	74.4 ± 34.1	0.0009***
Maximum hyoid depression angle (°)	7.5 ± 3.0	6.5 ± 4.6	0.0503
Time to maximum hyoid depression angle (ms)	53.1 ± 25.5	78.2 ± 30.3	0.0013*
Maximum hyoid retraction angle (°)	52.1 ± 4.8	39.8 ± 4.7	<0.0001***
Time to maximum hyoid retraction angle (ms)	52.2 ± 15.9	84.6 ± 30.7	<0.0001***
Maximum opercular expansion (mm)	16.2 ± 0.9	19.6 ± 4.7	0.0042**
Maximum opercular expansion (BL)	0.179 ± 0.004	0.198 ± 0.018	<0.0001***
Time to maximum opercular expansion (ms)	52.8 ± 12.9	87.4 ± 31.4	<0.0001***

Table 2.2: Displacement and timing variables associated with feeding kinematics for *Lentipes concolor* and *Awaous guamensis*. Values are means ± standard deviation. BL is the total body length. In statistical comparisons, * indicates significant difference at $P < 0.05$, ** at $P < 0.01$, and *** at $P < 0.001$ (Mann-Whitney *U*-test). Note: average values differ from maximum values in Figure 4 because the time of maxima differs among different trials.

Maximum gape angle was greater for *L. concolor* than *A. guamensis* ($43.8 \pm 13.7^\circ$ vs. $32.5 \pm 16.0^\circ$, $P = 0.0003$; Table 2.2 and Figure 2.3). *Lentipes concolor* also opened the mouth to maximum gape more than twice as quickly as *A. guamensis* (26.1 ± 12.7 ms vs. 54.4 ± 27.2 ms, $P < 0.0001$; Table 2.2). Among all the timing variables, the maximum gape is the first to be reached in the feeding strike (Table 2.2 and Figure 2.4); therefore, the maximum surface area of the mouth orifice would constrain both the maximum size of prey item (Hill et al., 2004) and the maximum water flow entering the orifice (Norton and Brainerd, 1993; Cook, 1996).

Gape angle is produced through rotations contributed by both the lower and upper jaws. Motions of both elements were greater and produced more quickly in *L. concolor*. The mandible of *L. concolor* exhibited greater and faster depression during mouth opening than that of *A. guamensis* ($37.1 \pm 9.8^\circ$ vs. $24.9 \pm 14.6^\circ$, $P < 0.0001$, and 31.5 ± 13.4 ms vs. 61.3 ± 27.4 ms, $P < 0.0001$, respectively; Table 2.2 and Figure 2.3). The maximum mandibular depression angle was reached slightly after the maximum gape angle apparently because motions of the upper jaw caused overall gape to close while the lower jaws were still opening. In both species, maximum premaxillary protrusion is realized near the end of the feeding strike, although this motion appears to plateau substantially after the midpoint of the feeding cycle (Figure 2.3). Like mandibular depression, *L. concolor* showed greater and faster premaxillary protrusion than *A. guamensis* (0.023 ± 0.006 BL vs. 0.016 ± 0.006 BL, $P < 0.0001$, and 51.6 ± 21.3 ms vs. 80.9 ± 30.7 ms, $P < 0.0001$, respectively; Table 2.2). The premaxilla of both species remained protruded until well after the end of the strike (i.e., mouth closed). *Lentipes*

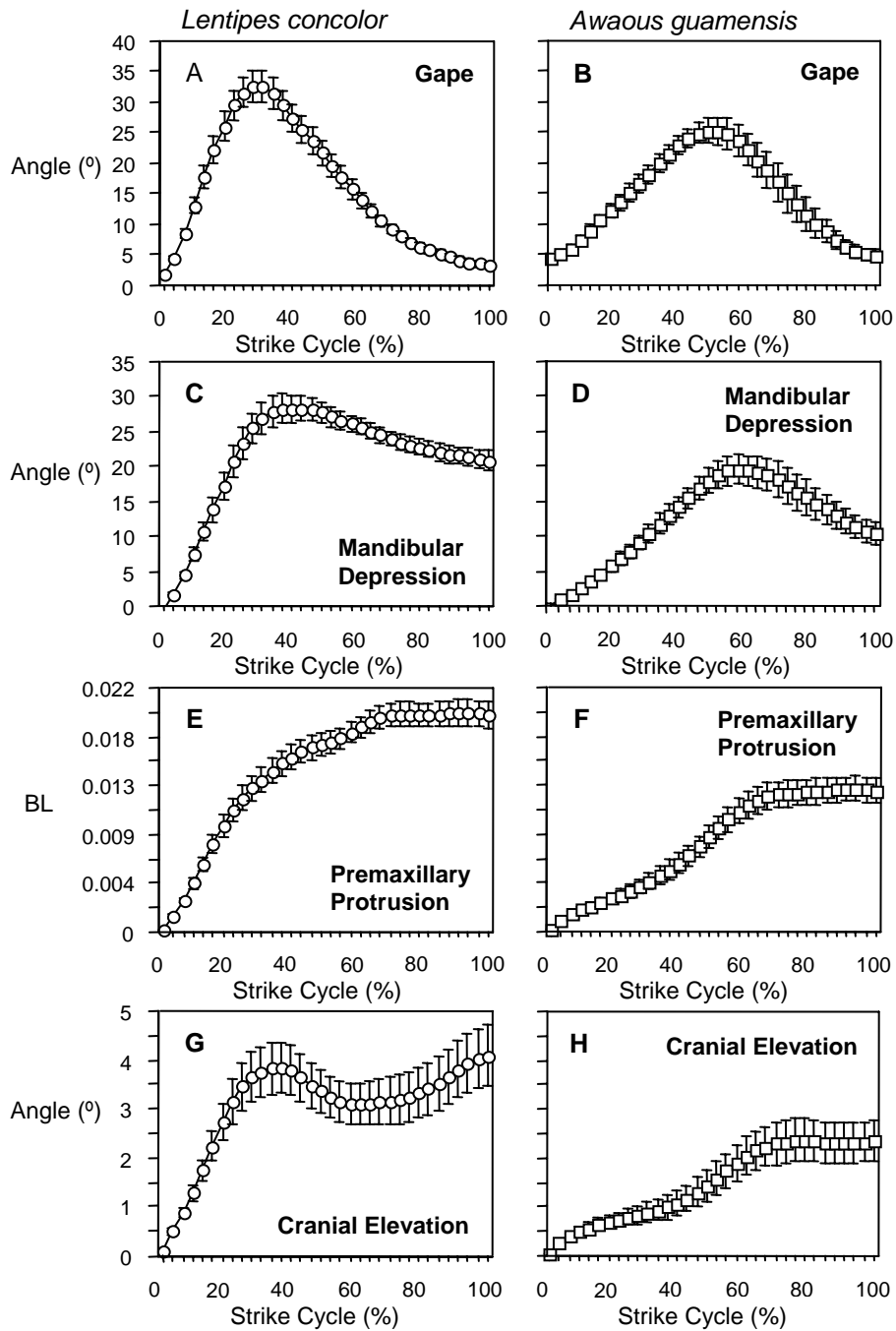


Figure 2.3: Kinematic profiles (gape (A and B), mandibular depression (C and D), premaxillary protrusion (E and F), and cranial elevation (G and F)) of feeding strike by *Lentipes concolor* and *Awaous guamensis*.

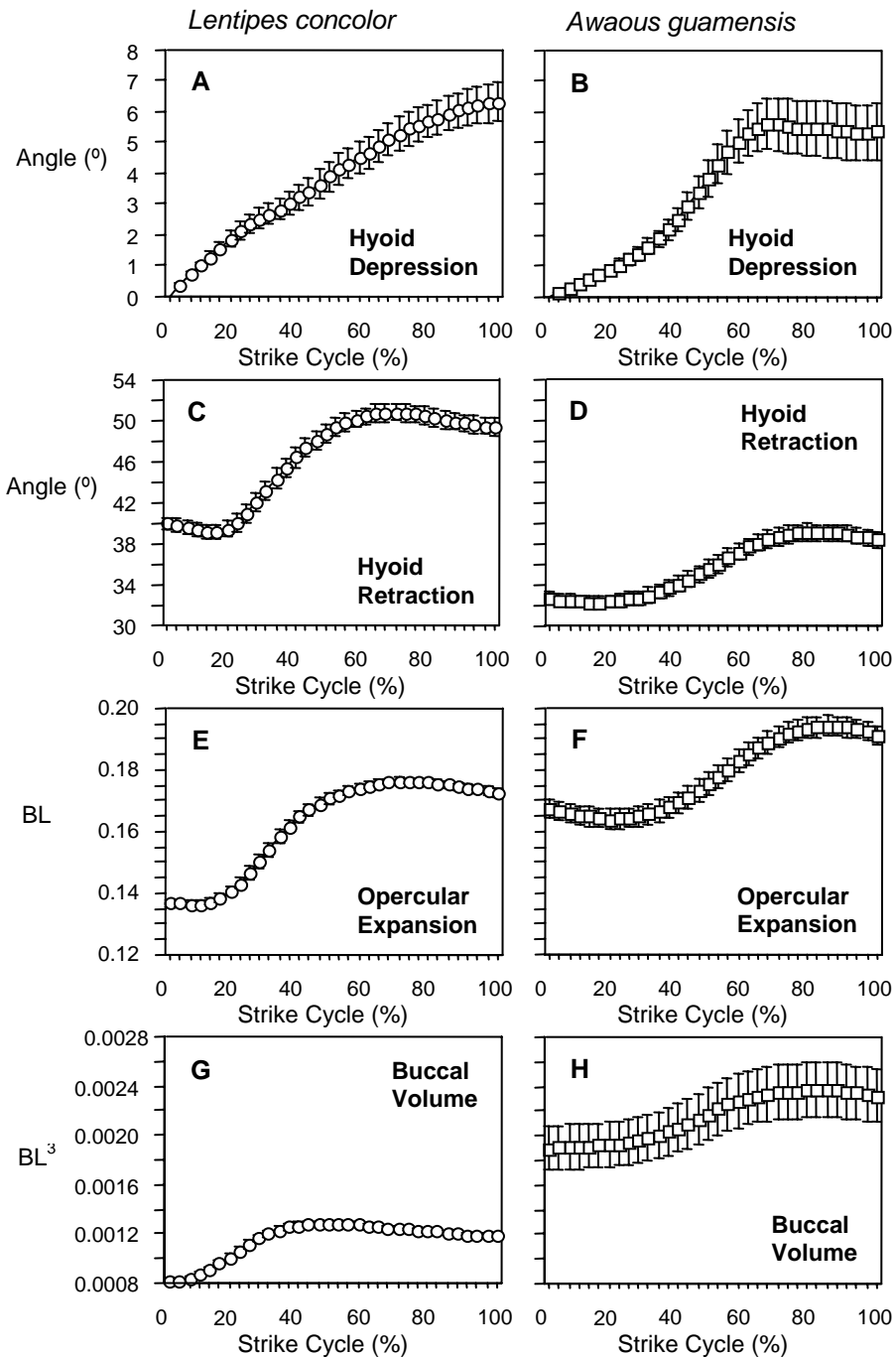


Figure 2.4: Kinematic profiles (hyoid depression (A and B), hyoid retraction (C and D), and opercular expansion (E and F)) of feeding strike, and buccal volume change during feeding strike (G and H) by *Lentipes concolor* and *Awaous guamensis*.

concolor also has more than twice the maximum cranial elevation of *A. guamensis* ($7.1 \pm 3.3^\circ$ vs. $3.1 \pm 2.3^\circ$, $P < 0.0001$: Table 2.2), and the maximum angle for cranial elevation was reached much more quickly for *L. concolor* than *A. guamensis* (47.0 ± 24.0 ms vs. 74.4 ± 34.1 ms, $P = 0.0009$: Table 2.2). Although there are some differences in kinematic profiles between species, cranial elevation motions roughly coincide with those of mandibular depression, upper jaw protrusion, and hyoid depression (Figures 2.3, 2.4) potentially synergistically powering buccal volume expansion through this synchronized action.

Both species shared similar maxima for the hyoid depression angle ($7.5 \pm 3.0^\circ$ for *L. concolor* and $6.5 \pm 4.6^\circ$ for *A. guamensis*, $P = 0.0503$: Table 2.2). However, profiles of the hyoid depression movements showed some differences, as the hyoid depressed essentially continually in *L. concolor*, but depression reached a plateau approximately three quarters of the way through the cycle in *A. guamensis* (Figure 2.4). Kinematic differences for the hyoid between species seemed much more significant in the ventral view. The differences in the hyoid retraction angle during a feeding strike were about 23% of the maximum (about 12° between the maximum and minimum) for *L. concolor* and about 17% of the maximum (about 7° between the maximum and minimum) for *A. guamensis* (Table 2.2 and Figure 2.4). The time to reach the maximum hyoid retraction angle was faster for *L. concolor* than *A. guamensis* (52.2 ± 15.9 ms and 84.6 ± 30.7 ms, respectively, $P < 0.0001$: Table 2.2). Because of the linkage between the hyoid and operculum, the retraction of the hyoid actuates the lateral expansion of the operculum (Figure 2.4). The differences in the opercular expansion during a feeding strike were

about 23% of the maximum opercular expansive width (approximately 0.04 BL between the maximum and minimum in width over the total body length of the fish) for *L. concolor* and about 16% of the maximum (approximately 0.03 BL between the maximum and minimum) for *A. guamensis* (Figure 2.4). In addition, *L. concolor* showed faster opercular expansion than *A. guamensis* (52.8 ± 12.9 ms vs. 87.4 ± 31.4 ms, respectively, $P < 0.0001$: Table 2.2). Although the gape cycle and time to maximum gape angle for *L. concolor* (77.7 ± 26.8 ms and 26.1 ± 12.7 ms, respectively: Table 2.2) were significantly faster than those for *A. guamensis* (106.8 ± 31.5 ms and 54.4 ± 27.2 ms, respectively, with $P = 0.0005$ and $P < 0.0001$, respectively: Table 2.2), there was no significant difference in the time to jaw closure from the time at maximum gape ($P = 0.8572$: Table 2.2). Thus, jaw closing performance does not appear to contribute significantly to differences in the capacity of these species to capture prey by suction.

Suction pressure estimates

The speed of water flow (v) induced near the mouth orifice by the feeding strike was calculated and compared between species. The time to the maximum gape angle was used for the time to gape change (T_G), and the maximum gape was used for calculation of the surface area of the mouth orifice (R_G) required for Eq. 2. Following the kinematic profile of buccal volume change, the change in volume between the beginning of the feeding strike and maximum gape was calculated allowing further calculation of the speed of induced water flow. *Lentipes concolor* showed faster flow than *A. guamensis* (8.09 ± 5.46 BL/s vs. 4.79 ± 2.85 BL/s, respectively, $P = 0.0133$, and 0.77 ± 0.54 m/s vs. 0.35 ± 0.23 m/s, respectively, $P = 0.0013$: Table 2.3).

Suction flow variable	<i>L. concolor</i> (N = 35)	<i>A. guamensis</i> (N = 28)	P value
Flow speed (m/s)	0.77 ± 0.54 (N = 33)	0.35 ± 0.23	0.0013**
Flow speed (BL/s)	8.09 ± 5.46 (N = 33)	4.79 ± 2.85	0.0133*
Maximum gape (mm)	5.04 ± 1.00	4.17 ± 1.42	0.006**
Maximum gape (BL)	0.056 ± 0.099	0.042 ± 0.010	<0.0001***
Maximum gape area (mm ²)	20.7 ± 8.2	15.1 ± 8.7	0.0413*
Maximum gape area (BL ²)	0.0026 ± 0.0009	0.0014 ± 0.0010	<0.0001***

Table 2.3: Maximum gape and flow speed at the maximum gape for *Lentipes concolor* and *Awaous guamensis*. Values are means ± standard deviation. BL is the total body length. In statistical comparisons, * indicates significant difference at $P < 0.05$, ** at $P < 0.01$, and *** at $P < 0.001$ (Mann-Whitney U -test).

Compared to *in vivo* measurements of suction flow speed previously measured in other species (e.g., 0.25 m/s in *Lepomis*: Lauder and Clark, 1984; 0.08 m/s in *Lepomis*: Ferry-Graham et al., 2003), our calculated estimates of flow speeds were faster for both goby species. According to Ferry-Graham et al. (2003), water velocity at maximum gape seems to be the maximum water velocity induced by fishes. Part of difference in flow speed induced by the two goby species can be attributed to differences in their speeds of mouth opening and sizes of their gapes. *Lentipes concolor* had a greater maximum gape normalized for total body length (0.056 ± 0.099 BL for *L. concolor* vs. 0.042 ± 0.010 BL for *A. guamensis*, $P < 0.0001$: Table 2.3), and, as a result, a greater surface area of the orifice normalized for square of total body length (0.0026 ± 0.0009 BL² vs. 0.0014 ± 0.0010 BL², respectively, $P < 0.0001$: Table 2.3). Substituting the flow speeds estimated into Bernoulli's principle (Eq. 1) gives pressure differentials of 0.2965 kPa/BL³ for *L. concolor* and 0.06215 kPa/BL³ for *A. guamensis*. Comparison of these values predicts that *L. concolor* can generate about 4.8 times greater suction pressure than *A. guamensis*.

Discussion

Relationship of differences in feeding performance to habitat and jaw morphology in Hawaiian climbing gobies

Because adult *L. concolor* typically live in streams with faster flow speeds, whereas *A. guamensis* often live in the slower flow of lower stream reaches, we predicted that *L. concolor* would exhibit faster feeding motions than *A. guamensis*. Our results agreed with this prediction; however, the difference in performance was concentrated in a specific portion of the feeding cycle. Our results show that *L. concolor* achieve maximum gape angle in less than one half the time required for *A. guamensis*, and that *L. concolor* reach the maximum of all kinematic angles that contribute to mouth opening (e.g., mandibular depression, premaxillary protrusion, cranial elevation) faster than *A. guamensis*. However, the two species do not differ in the time it takes to close the jaws once maximum gape has been reached. Thus, differences in suction feeding performance between these species are more closely related to jaw opening rather than jaw closing or, in other words, to prey acquisition rather than retention of prey in the mouth by closing the jaws around it. The differences we observed were measured in still water, and it would be useful to verify their performance during feeding in flows similar to those encountered by the two species in their natural habitats. However, the functional differentiation we found between *L. concolor* and *A. guamensis* suggests that, in species living in fast flow, the potential for prey to be lost from the buccal cavity differs little from that encountered by species living in slower flow. In contrast, the increased

challenges of prey acquisition in faster flowing water may be met with higher levels of feeding performance.

In addition to differences in the speed of jaw opening between *L. concolor* and *A. guamensis*, we found that even when striking at identical prey in identical water flow conditions (still water), *L. concolor* achieved a significantly wider gape (almost 35% greater) than *A. guamensis*. Because suction pressure is inversely related to the size of the mouth orifice (Eq. 4), it might be expected that *L. concolor* would, as a result, generate lower suction pressures than *A. guamensis*. However, this is not what we found. Instead, our geometric modeling of suction pressure indicates that *L. concolor* might generate pressure differentials almost 5 times greater than those of *A. guamensis*. Our anatomical models indicate that *L. concolor* are able to overcome limitations to suction pressure induced by a large gape as a result of their extremely fast jaw movements. The Hagen-Poiseuille equation indicates that, though suction pressure is inversely related to gape size, it is directly related to the velocity of flow that can be generated. The rapid jaw movements of *L. concolor* enable rapid increases in buccal volume (Eq. 2 & 3), facilitating rapid flow speeds and elevating the pressure differential generated. Thus, *L. concolor* can achieve higher suction pressure differentials than *A. guamensis* despite their larger gape size, improving their ability to acquire large prey items even in fast flowing water. These geometric estimates of suction pressure have yet to be verified by more direct experimental methods, such as buccal pressure transducer implants (Lauder, 1980; Carroll et al., 2004; Higham et al., 2006) or particle image velocimetry (Ferry-Graham and Lauder, 2001; Ferry-Graham et al., 2003; Day et al., 2005; Higham et al., 2005,

2006a, 2006b), though the use of these methods is complicated by the small body size and typical benthic feeding habits of our study species.

Morphological differences in the jaw lever systems of *L. concolor* and *A. guamensis* may contribute to the differences in the speeds of their jaw movements. These species showed no difference in jaw closing speeds and, correspondingly, did not differ significantly in velocity advantage for jaw closing as calculated from the lever systems of their jaw skeleton. However, differences in the velocity advantage for jaw opening between *L. concolor* and *A. guamensis* are proportionally greater than those for jaw closing (10% vs. 5%), and are also in the direction predicted to convey faster jaw motion to the species living in faster flow (*L. concolor*). Although these patterns are suggestive, skeletal components of lever systems cannot completely predict function, as the arrangements and dimensions of muscles and tendons are also critical to mechanical performance (Westneat, 2003; Chapter 3). More complete evaluation of the morphological basis for feeding performance differences between *L. concolor* and *A. guamensis* will require examination of those components of the feeding apparatus of these fishes, but available skeletal data suggest this is a promising avenue of investigation.

Future directions for ecological and evolutionary studies of Hawaiian stream goby feeding

The feeding performance of *L. concolor* appears to suit it well to life in fast flowing water, but would not necessarily suit it poorly in habitats with slower flow. In this context, it is somewhat puzzling that the distributions of adult *L. concolor* and *A.*

guamensis do not overlap in streams on the Island of Hawai'i, and that adult *L. concolor* are absent from lower stream reaches where *A. guamensis* are common (Macioleck, 1977; Blob et al., 2006). Given the similarities of the diets of these species (Kido, 1996), it is possible that *L. concolor* might be excluded from lower stream reaches as a result of direct or indirect interactions (e.g., resource partitioning; Takamura, 1984; Vadas, 1990; Bouton et al., 1997) with *A. guamensis*, though the nature of such interactions is uncertain. However, lower stream flows induced by anthropogenic means (e.g., water diversion or damming; Bain et al., 1988; Brasher, 1996; Way et al., 1998) could reduce the limits to upstream migration by *A. guamensis* due to its limited climbing ability (Brasher, 1996; Blob et al., 2006; in press). The distribution of *L. concolor* might be expected to shift further upstream in response and, alternatively, might be diminished due to loss of suitable habitat.

Given that we have examined the feeding kinematics of only two goby species, it is uncertain which species might show performance and function closer to the ancestral condition, and which, if either, might be viewed as possessing adaptations related to its specific environment (Garland and Adolph, 1994). Gobies are one of the most remarkably diverse and speciose clades of vertebrates with over 2000 species in 268 genera worldwide (Lauder and Liem, 1983; Nelson, 1994; Thacker, 2003), and our data represent a starting point for a broader phylogenetic examination of functional performance in this group (Westneat, 1994, 1995). With rapidly increasing knowledge of the phylogenetic relationships of these species (Parenti and Thomas, 1998; Thacker,

2003), evolutionary studies of their functional specializations promise to generate a wide range of insights into the evolution of functional performance.

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CHAPTER THREE

JAW LEVER ANALYSIS OF HAWAIIAN STREAM FISHES: A SIMULATION STUDY OF MORPHOLOGICAL DIVERSITY

Introduction

Gobioid fishes are a remarkably speciose group of teleosts with more than 2000 species in 268 genera worldwide that exhibit a wide range of niches, behaviors, and life histories (Nelson, 1994; Thacker, 2003). In perennial streams of the Hawaiian islands, the native ichthyofauna consists of five gobioid species (four gobiids and one eleotrid: Fitzsimons et al., 1993) that exhibit great variability in their habitat and behaviors (Yamamoto and Tagawa, 2000). For example, of the five native Hawaiian species, three (*Sicyopterus stimpsoni*, *Lentipes concolor*, and *Awaous guamensis*) exhibit waterfall-climbing ability during at least part of their ontogeny. Despite the rigorous demands of this behavior that might be expected to limit functional variation in these fishes, two distinct modes of climbing behavior have been recognized in these species (“inching” climbing in *S. stimpsoni*, and “powerburst” climbing in *L. concolor* and *A. guamensis*: Schoenfuss and Blob, 2003; Blob et al., 2006, in press). These different behaviors have been associated with differences in the ecological distributions of these species in streams (Blob et al., 2006), as well as anatomical and physiological specializations (Schoenfuss et al., 1997; Cediél et al., 2007; Maie et al., 2007).

In addition to variation in the locomotor system, functional variation in fishes is often evident in the feeding system, with trophic performance frequently correlated with both morphological and ecological specializations (Bouton et al., 1997, 1998, 2002;

Wainwright et al., 2004). Although most Hawaiian stream gobioids have a ventrally positioned mouth, differences in their diets have been identified that have been associated with morphological differences between these species (Kido, 1996a, 1996b, 1997). For example, *S. stimpsoni* feed by scraping algae from rock surfaces using a highly protrusible premaxilla equipped with rows of tricuspid teeth (Kido, 1996b; Julius et al., 2005; Fitzsimons et al., 2003). Both *A. guamensis* and *L. concolor* have been suggested to consume similar proportions of animal and plant materials (Kido, 1996b), but typically live in different habitats, with *A. guamensis* inhabiting slower, lower stream reaches and *L. concolor* inhabiting faster, upper stream reaches (Schoenfuss and Blob, 2007). Correspondingly, *L. concolor* show a jaw skeleton with a lever system designed for faster jaw opening than *A. guamensis*, and exhibit faster jaw opening during suction feeding (Chapter 2). *Stenogobius hawaiiensis* have conical teeth on the premaxilla and dentary, and feed by ingesting stream bottom sediment and filtering out primarily plant materials. Finally, *E. sandwicensis* consume a greater proportion of animal materials than other Hawaiian stream gobiids (56.2% dry biomass of the total gut content) and are highly piscivorous (Kido, 1996b; Tate, 1997; Yamamoto and Tagawa, 2000). They have conical teeth and are the only Hawaiian stream gobioid fish in which the mouth is in a sub-dorsal position.

The differences in feeding behavior and performance just described among Hawaiian stream gobies were related primarily to differences in the skeletal anatomy of these species (Kido, 1996b). However, like all anatomical lever systems, the performance of the jaws during feeding in these fishes could depend substantially on the

proportions and configurations of their jaw muscles (Wainwright and Richard, 1995; Westneat, 2003). Given the great variety of feeding habits of Hawaiian gobies, a great range of feeding performance might be expected. In this study, we combine measurements of both skeletal and muscular anatomy to predict jaw closing performance of these fishes using a previously published anatomical model (Westneat, 2003), in order to test whether differences in feeding habits are reflected in the differing anatomical performance of these species.

Materials and Methods

Species collection and functional comparisons

Specimens of five native Hawaiian gobioid species (*S. stimpsoni*, *L. concolor*, *A. guamensis*, *S. hawaiiensis*, and *E. sandwicensis*) were captured (Clemson AUP# 40061 and 50089) while snorkeling using an o'pae net (a fine, spherically shaped mesh with a narrow opening at the top of a bowl shaped basket). Collections were made from native streams of these fishes on the Islands of Hawai'i and Kaua'i during field seasons between 2003 and 2006 (Table 3.1). Specimens were preserved in 70% ethanol, after which the jaw muscles and skeleton were dissected under a dissecting scope (Nikon SMZ 1000) and photographed using a digital camera (Nikon CoolPix 4300) in order to collect morphological measurements for input into the Westneat (2003) model of jaw performance.

Specimens	<i>N</i>	Locality (in Hawai'i)	Locality (in Kaua'i)	Season
<i>S. stimpsoni</i>	34	Nanue stream	Hanakapi'ai & Limahuli streams	2004
<i>L. concolor</i>	23	Hakalau, Kamae'e, Manoloa, & Nanue streams	Hanakapi'ai stream	2004-2006
<i>A. guamensis</i>	19	Hakalau & Nanue streams Waiakea Pond	Hanakapi'ai & Limahuli streams	2004-2006
<i>S. hawaiiensis</i>	15	Waiakea Pond	None	2006
<i>E. sandwicensis</i>	13	Hakalau & Nanue streams Wailoa Pond	None	2003-2006

Table 3.1: List of specimens, native habitats (collection sites) and field seasons.

Specimens of *S. stimpsoni* were from both upper and lower reaches (relative to waterfalls) of indicated streams from the two islands (Hawai'i and Kaua'i). Specimens of *L. concolor* were from only upper stream reaches higher than any other species. Specimens of the remaining three species were from lower stream reaches or water pools (Waiakea Pond and Wailoa Pond of the Island of Hawai'i).

Simulation of mandibular movement

The adductor mandibulae muscles are the major force-generating muscle complex powering jaw closing in teleosts during feeding strikes. This muscle complex pulls the mandible around a point of rotation at the quadratomandibular joint in a third-order lever mechanism (Westneat, 2003). To evaluate jaw closing performance of Hawaiian gobies, measurements of the muscles and their attachments for each species were input into a simulation of a jaw closing event using MandibLever 3.0, software developed by M. Westneat (2003) and available at (<http://www.fieldmuseum.org/>). Based on these measurements of the feeding apparatus (detailed below) and non-linear contractile properties of muscle fibers (e.g., the Hill equation; $F = (1-V)/(1+V/k)$ with $k = 0.25$: Westneat, 2003), the transmission of speed and force, as well as other functional parameters associated with the jaws, can be calculated using this simulation (Westneat,

2003). Initial conditions are required for several parameters in these calculations, which estimate aspects of functional performance through changes in parameters (e.g., F and V) in the Hill equation during a jaw closing event. Following conventions of Westneat (2003), these parameters included maximum isometric force per unit area of muscle (F_{max}), which was input with an F/F_{max} value ranging between 0.05 to 0.8, and estimated maximum velocity of muscle contraction (V_{max}), which was input with a V/V_{max} ranging between 0.05 to 0.79 for the simulation. Also following Westneat's (2003) conventions, a shortening of 10 length/sec ($= V_{max}$) was assumed based on fast twitching white muscle fibers in fish jaw muscle, and a maximum isometric stress (i.e., force production per unit cross-sectional area of muscle) of 100 kPa was used as a standard value. In order to obtain consistent increments in time, mathematical transformations were performed using curvilinear regressions. Given jaw closing durations found in *in vivo* feeding kinematics of *L. concolor* and *A. guamensis* (52 ms and 54 ms, respectively; Chapter 2), a 50 ms total duration was assumed, and values of calculated variables were plotted over fractional (%) increments of time through this jaw closing duration.

Four performance variables were computed for each muscle division using measurements from one side of the head (unilateral performance variables): (1) maximum force output, normalized to body size (i.e., divided by BL^3); (2) maximum angular velocity; (3) minimum and maximum effective mechanical advantages (*EMA*), each of which is calculated as the product of the skeletal lever ratio for jaw closing and the sine of the angle of muscle insertion on the mandible; (4) maximum mandibular power output, specific to muscle size and also normalized to body size. Calculations

were performed starting with an initial opening of the mandible at 30° and progressed as the jaw angle closed toward 0°. This angular range seems to be appropriate based on the kinematics of mandibular depression previously evaluated for *L. concolor* and *A. guamensis* (Chapter 2). Performance values were compared using one-way ANOVA and Fisher's LSD post hoc tests at $\alpha = 0.05$ level to evaluate the significance of differences in performance between species.

Morphological measurements of the adductor mandibulae muscles and jaw apparatus

The adductor mandibulae muscles are situated on superficial aspect of the cranium of teleosts (Winterbottom, 1974; Gosline, 1986). Although a few variations in the muscle complex (e.g., size and point of insertion) can be observed among the five Hawaiian gobies (Tables 3.2, 3.3 and 3.4), basic external configurations among them are extremely similar. The adductor mandibulae muscles are divided into three parts based on differing insertions on the feeding apparatus: A1, A2, and A3. The A1 division is the most superficial and inserts on the maxilla. Because of this distinct insertion, the A1 likely performs a different function than the other adductor mandibulae subdivisions (Gosline, 1986). Its performance was not modeled by Westneat (2003) and was not evaluated in this study. Deep to the A1 division, A2 originates on the laterocaudal surface of the preoperculum, and inserts on the coronoid process of the dentary. The A2 further subdivides into several bundles (i.e., dorsal and ventral bundles) each possessing separate tendons with similar lengths, but functions of these two smaller subdivisions are typically similar (Westneat, 2003). The A3 is the deepest muscle of the adductor mandibulae

muscles, and further subdivides into three smaller bundles originating on the broad fossa of the metapterygoid, the laterocaudal aspect of the symplectic, and the lateroanterior surface of the preoperculum. These smaller bundles of the A3 division fuse together to form a single tendon inserting on the medial aspect of the articular of the mandible.

Pinnation of these muscles appears negligible in Hawaiian gobies.

Species	BL (cm)	A2 (g)	A3 (g)	A2/BL ³ (g/cm ³)	A3/BL ³ (g/cm ³)
<i>S. stimpsoni</i> (N=34)	8.56 ± 2.04	0.0032 ± 0.0021	0.0015 ± 0.0009	4.38 ± 1.15, d	2.09 ± 0.54, c
<i>L. concolor</i> (N=23)	6.94 ± 1.14	0.0021 ± 0.0014	0.0013 ± 0.0009	5.44 ± 1.42, d	3.16 ± 0.97, c
<i>A. guamensis</i> (N=19)	8.89 ± 2.74	0.0192 ± 0.0319	0.0096 ± 0.0156	16.30 ± 5.12, b	8.30 ± 2.69, b
<i>S. hawaiiensis</i> (N=15)	6.42 ± 0.94	0.0034 ± 0.0017	0.0020 ± 0.0009	11.96 ± 1.88, c	7.12 ± 1.12, b
<i>E. sandwicensis</i> (N=13)	9.84 ± 2.59	0.0442 ± 0.0429	0.0210 ± 0.0195	35.83 ± 1.05, a	17.76 ± 4.88, a

Table 3.2: Body length (cm), muscle mass (g), and muscle mass normalized to body size expressed as BL³ (g/cm³, note: these values are multiplied by 10⁻⁶) for the adductor mandibulae muscle divisions of five native Hawaiian gobies.

Values are means ± standard deviations. Species are grouped into a, b, c, and d ranks (a to d, in a decreasing manner) based on ANOVA ($F = 137.602$, $P < 0.0001$ for A2 (g/cm³), and $F = 139.765$, $P < 0.0001$ for A3 (g/cm³)) and Fisher's LSD ($\alpha = 0.05$) post hoc tests.

Species	A2 Length (cm)	A3 Length (cm)	A2 Length/BL	A3 Length/BL
<i>S. stimpsoni</i> (N=34)	0.603 ± 0.157	0.667 ± 0.163	0.070 ± 0.006, c	0.078 ± 0.006, c
<i>L. concolor</i> (N=23)	0.407 ± 0.090	0.508 ± 0.117	0.058 ± 0.006, d	0.073 ± 0.006, d
<i>A. guamensis</i> (N=19)	0.859 ± 0.363	0.927 ± 0.347	0.095 ± 0.012, b	0.103 ± 0.008, b
<i>S. hawaiiensis</i> (N=15)	0.429 ± 0.072	0.510 ± 0.080	0.067 ± 0.006, c	0.080 ± 0.006, c
<i>E. sandwicensis</i> (N=13)	1.007 ± 0.265	1.152 ± 0.317	0.104 ± 0.014, a	0.118 ± 0.016, a

Table 3.3: Muscle length (cm) and muscle length normalized to body length of the adductor mandibulae muscle division A2 and A3 of five native Hawaiian gobies. Values are means ± standard deviations. Species are grouped into a, b, c, and d ranks (a to d, in a decreasing manner) based on ANOVA ($F = 86.062$, $P < 0.0001$ for A2 length/BL, and $F = 93.928$, $P < 0.0001$ for A3 length/BL) and Fisher's LSD ($\alpha = 0.05$) post hoc tests.

Species	Close Lever Ratio A2	Close Lever Ratio A3
<i>S. simpsoni</i> (N=34)	0.373 ± 0.059, c	0.458 ± 0.054, b
<i>L. concolor</i> (N=23)	0.427 ± 0.058, b	0.380 ± 0.060, a
<i>A. guamensis</i> (N=19)	0.424 ± 0.034, b	0.421 ± 0.042, a
<i>S. hawaiiensis</i> (N=15)	0.489 ± 0.046, a	0.279 ± 0.050, c
<i>E. sandwicensis</i> (N=13)	0.348 ± 0.046, c	0.389 ± 0.036, a

Table 3.4: Jaw closing lever ratio (mechanical advantage) for A2 and A3 based only on the skeletal components of the feeding apparatus. Values are means ± standard deviations. Species are grouped into a, b, and c ranks (a to c, in a decreasing manner) based on ANOVA ($F = 18.571$, $P < 0.0001$ for A2, and $F = 33.828$, $P < 0.0001$ for A3) and Fisher's LSD ($\alpha = 0.05$) post hoc tests.

The superficial aspect of the A2 division, where the muscle has the greatest long axis, was used for measurement of A2 length. After measuring its length including its tendon, it was removed and its mass was measured to the nearest 0.0001g with a digital balance (Denver Instrument). After the removal of A2, the length and mass of A3 were measured in a similar manner. Points of origin for both A2 and A3 were determined by locating areas of origin on the cranium, where their muscle fibers run parallel to their respective tendons. Using NIH Image software for Apple Macintosh (developed by the U.S. National Institutes of Health and available at <http://rsb.info.nih.gov/nih-image/>), twelve linear distances in the cranium of each species (Figure 3.1) were measured from digital photographs: (1) in-lever arm for A2, distance between the quadratomandibular joint and the superior tip of the coronoid process of the dentary, where A2 inserts; (2) in-lever arm for A3, distance between the quadratomandibular joint and the medial surface of the articular, where A3 inserts; (3) in-lever arm for jaw opening, distance between the quadratomandibular joint and the posteroventral aspect of the articular, where the interoperculomandibular ligament inserts; (4) out-lever arm of the mandible, distance

between the quadratomandibular joint and the anterior tip of the dentary; (5) A2 muscle length; (6) A3 muscle length; (7) tendon length for A3; (8) distance between A2 origin and the quadratomandibular joint; (9) distance between A3 origin and the quadratomandibular joint; (10) distance between A2 and A3 insertions; (11) dorsal length of the mandible, distance between the superior tip of the coronoid process of the dentary and the anterior tip of the dentary; (12) ventral length of the mandible, distance between the posteroventral aspect of the articular to the anterior tip of the dentary. Body length

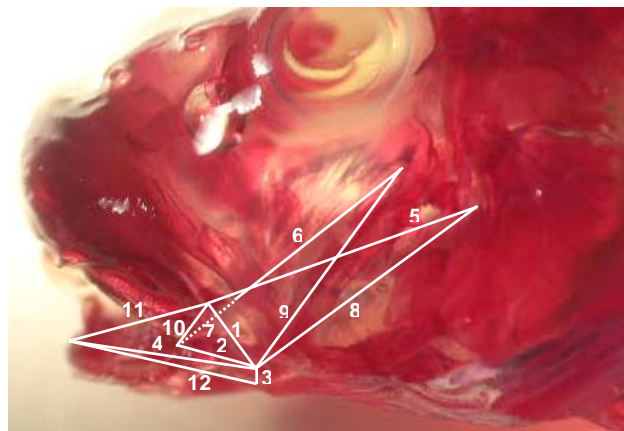


Figure 3.1: Linear measurements in the feeding apparatus (cranium) of *Sicyopterus stimpsoni* used in the mandibular lever model. (Note: (1) in-lever arm for A2; (2) in-lever arm for A3; (3) in-lever arm for jaw opening; (4) out-lever arm of the mandible; (5) A2 muscle length; (6) A3 muscle length; (7) tendon length for A3; (8) distance between A2 origin and the quadratomandibular joint; (9) distance between A3 origin and the quadratomandibular joint; (10) distance between A2 and A3 insertions; (11) dorsal length of the mandible; (12) ventral length of the mandible).

(from the tip of snout to the tip of caudal fin) of each specimen was also measured. In addition to being input into the Westneat (2003) model, masses of A2 and A3, as well as linear measurements, could then be normalized for body size differences among

individuals (linear measurements divided by body length, L, and masses divided by L³). These values were then compared using one-way ANOVA and Fisher's LSD post hoc test at $\alpha = 0.05$ level to evaluate the significance of morphological differences between species.

Results

Analysis of mandibular movement

As the mandible closes, output force of both A2 and A3 increase linearly, starting with the lowest forces and ending with the highest forces (Figure 3.2). However, ANOVA indicates significant differences in the maximum output forces among species ($F = 23.156$, $P < 0.0001$ for output force of A2, and $F = 18.282$, $P < 0.0001$ for A3), with post hoc analysis showing that *S. stimpsoni* ($3.02 \times 10^{-5} \pm 1.41 \times 10^{-5}$ N/cm³ for A2, and $2.20 \times 10^{-5} \pm 1.09 \times 10^{-5}$ N/cm³ for A3) and *L. concolor* ($3.68 \times 10^{-5} \pm 1.13 \times 10^{-5}$ N/cm³ for A2, and $2.53 \times 10^{-5} \pm 7.46 \times 10^{-5}$ N/cm³ for A3) have the lowest output force potential among the five species (Table 3.5). In contrast, *A. guamensis* ($9.71 \times 10^{-5} \pm 6.35 \times 10^{-5}$ N/cm³ for A2, and $5.84 \times 10^{-5} \pm 3.94 \times 10^{-5}$ N/cm³ for A3), *S. hawaiiensis* ($7.96 \times 10^{-5} \pm 1.69 \times 10^{-5}$ N/cm³ for A2, and $5.18 \times 10^{-5} \pm 1.28 \times 10^{-5}$ N/cm³ for A3), and *E. sandwicensis* ($10.33 \times 10^{-5} \pm 4.07 \times 10^{-5}$ N/cm³ for A2, and $6.59 \times 10^{-5} \pm 2.81 \times 10^{-5}$ N/cm³ for A3) showed similarly high output force for both A2 and A3 divisions (Table 3.5). In addition, for all species, A2 generated approximately 1.5 times greater output force than A3 (Table 3.5).

Species	Maximum Output Force A2 (N/BL ³)	Maximum Output Force A3 (N/BL ³)
<i>S. stimpsoni</i> (N=34)	3.02 ± 1.41, b	2.20 ± 1.09, b
<i>L. concolor</i> (N=23)	3.68 ± 1.13, b	2.53 ± 7.46, b
<i>A. guamensis</i> (N=19)	9.71 ± 6.35, a	5.84 ± 3.94, a
<i>S. hawaiiensis</i> (N=15)	7.96 ± 1.69, a	5.18 ± 1.28, a
<i>E. sandwicensis</i> (N=13)	10.33 ± 4.07, a	6.59 ± 2.81, a

Table 3.5: Maximum jaw output force of A2 and A3, normalized to body size (note: these values are to be multiplied by 10⁻⁵). Values are means ± standard deviations. Species are grouped into a and b ranks (a to b, in a decreasing manner) based on ANOVA ($F = 23.156$, $P < 0.0001$ for A2, and $F = 18.282$, $P < 0.0001$ for A3) and Fisher's LSD ($\alpha = 0.05$) post hoc tests.

Inversely to the muscle force production, as the mandible closes its angular velocity exponentially decreases (Figure 3.2). *Sicyopterus stimpsoni* (2.51 ± 0.72 °/ms), *A. guamensis* (2.46 ± 1.05 °/ms), and *E. sandwicensis* (2.26 ± 0.44 °/ms) exhibited similar angular velocities of A2 at the beginning of mandibular closure that were faster than those of *L. concolor* and *S. hawaiiensis* (1.75 ± 0.53 °/ms and 1.33 ± 0.12 °/ms, respectively; $F = 10.903$, $P < 0.0001$: Table 3.6). However, all of the species exhibited similar angular velocity for A3 (Table 3.6). In addition, A3 produced up to twice as fast a velocity in jaw closing than A2 for all species (Table 3.6).

As the mandible closes, *EMA* of both A2 and A3 increased and reached a plateau near the first one-third of the cycle (Figure 3.2). For both minimum *EMA* of A2 at the beginning and maximum *EMA* of A2 at the end of the cycle, *S. hawaiiensis* had the highest values of all species (0.411 ± 0.050 for the minimum, and 0.477 ± 0.048 for the maximum: Table 3.7). Further, for the *EMA* of A2, *A. guamensis* (0.196 ± 0.093 for the minimum, and 0.267 ± 0.119 for the maximum) and *E. sandwicensis* (0.216 ± 0.043 for the minimum,

and 0.295 ± 0.047 for the maximum) both exhibited similar *EMAs* for A2 that were significantly lower than those of other species, indicating higher velocity advantages (Table 3.7). For the *EMA* of A3, *A. guamensis* again showed the lowest value

Species	Maximum Angular Velocity A2 (°/ms)	Maximum Angular Velocity A3 (°/ms)
<i>S. stimpsoni</i> (N=34)	2.51 ± 0.72 , a	3.22 ± 0.81
<i>L. concolor</i> (N=23)	1.75 ± 0.53 , b	2.80 ± 0.57
<i>A. guamensis</i> (N=19)	2.46 ± 1.05 , a	2.79 ± 1.11
<i>S. hawaiiensis</i> (N=15)	1.33 ± 0.12 , b	2.85 ± 0.64
<i>E. sandwicensis</i> (N=13)	2.26 ± 0.44 , a	2.90 ± 0.66

Table 3.6: Maximum values in angular velocity of A2 and A3 (°/ms). Values are means \pm standard deviations. Species are grouped into a and b ranks (a to b, in a decreasing manner) based on ANOVA ($F = 10.903$, $P < 0.0001$ for A2; there was no significance, $F = 1.472$, $P = 0.2166$ for A3 among species) and Fisher's LSD ($\alpha = 0.05$) post hoc tests.

Species	Minimum <i>EMA</i> 2	Maximum <i>EMA</i> 2	Minimum <i>EMA</i> 3	Maximum <i>EMA</i> 3
<i>S. stimpsoni</i> (N=34)	0.264 ± 0.071 , b	0.336 ± 0.071 , c	0.115 ± 0.028 , a	0.213 ± 0.053 , a
<i>L. concolor</i> (N=23)	0.298 ± 0.080 , b	0.380 ± 0.076 , b	0.127 ± 0.039 , a	0.226 ± 0.057 , a
<i>A. guamensis</i> (N=19)	0.196 ± 0.093 , c	0.267 ± 0.119 , d	0.092 ± 0.014 , b	0.151 ± 0.043 , b
<i>S. hawaiiensis</i> (N=15)	0.411 ± 0.050 , a	0.477 ± 0.048 , a	0.129 ± 0.037 , a	0.204 ± 0.048 , a
<i>E. sandwicensis</i> (N=13)	0.216 ± 0.043 , c	0.295 ± 0.047 , d	0.118 ± 0.034 , a	0.212 ± 0.050 , a

Table 3.7: Minimum and maximum values in effective mechanical advantage (*EMA*) of A2 and A3. Values are means \pm standard deviations. Species are groups into a, b, c, and d ranks (a to d, in a decreasing manner) based on ANOVA ($F = 21.636$, $P < 0.0001$ for minimum *EMA* of A2, $F = 17.843$, $P < 0.0001$ for maximum *EMA* of A2, $F = 4.270$, $P = 0.0031$ for minimum *EMA* of A3, and $F = 6.545$, $P = 0.0001$ for maximum *EMA* of A3) and Fisher's LSD ($\alpha = 0.05$) post hoc tests between species.

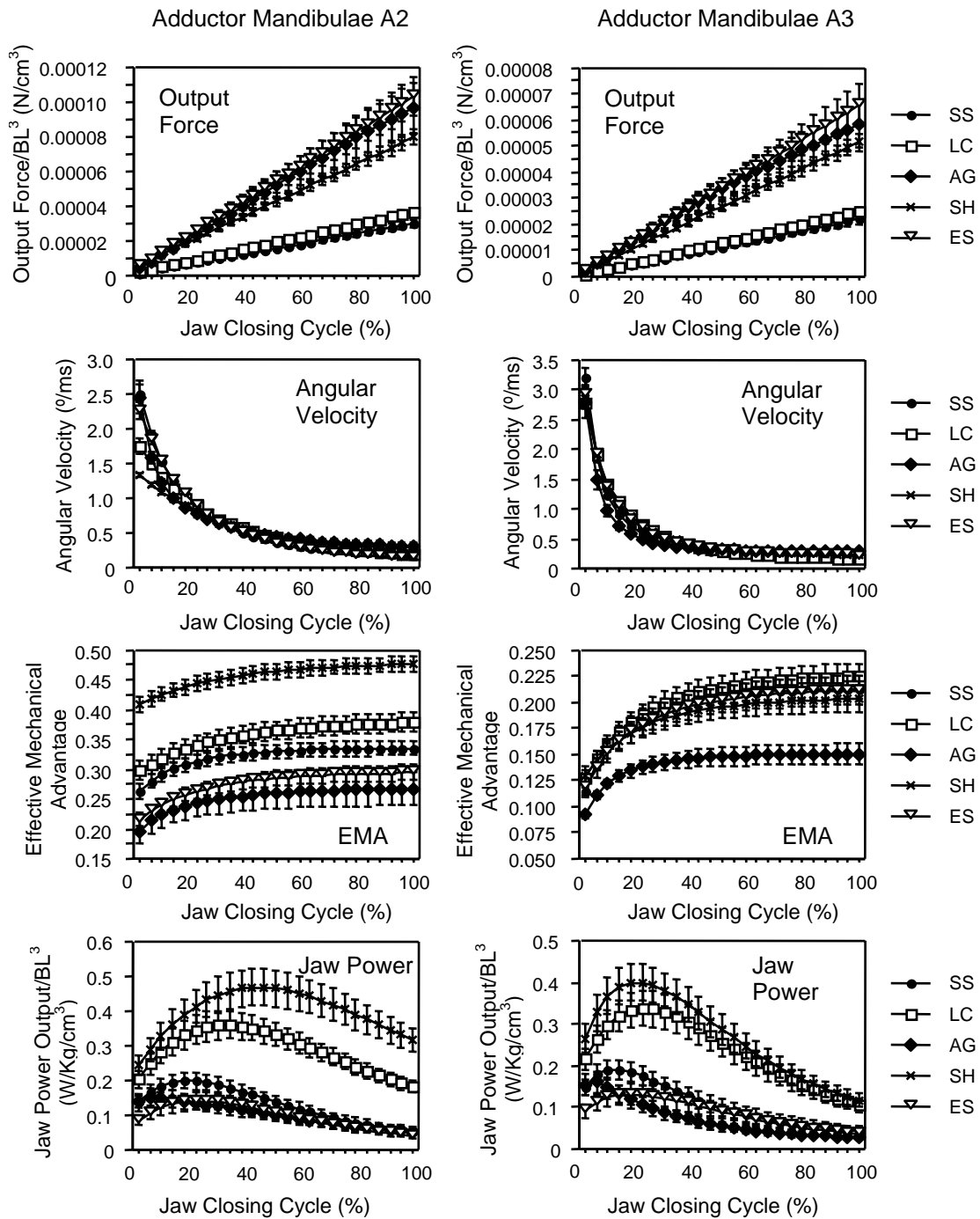


Figure 3.2: Performance variables (output force at the jaw tip, angular velocity, effective mechanical advantage, and jaw power output) of all five species of Hawaiian gobies during jaw closing cycle.

in the course of mandibular closing (0.092 ± 0.014 for the minimum, and 0.151 ± 0.043 for the maximum) and was the only species that deviated (by approximately 25%) from all other species (Table 3.7). As evident in output force and angular velocity, in all species A2 had higher mechanical advantage (and conversely lower velocity advantage) than A3, suggesting differentiation of their functional roles in jaw closing performance.

Because the jaw power is a product of output force and velocity (i.e., Power = $F*V$), its maximum value is reached during the course of the mandibular closing cycle rather than at its beginning or end (Figure 3.2). The timing of maximum power output for A2 differed between species occurring at about 20% of jaw closing cycle in *S. stimpsoni*, *A. guamensis*, and *E. sandwicensis*, and later at about 40-50% in *L. concolor* and *S. hawaiiensis*. Maximum power output for A3 was also early for *A. guamensis* at about 10% of the cycle, but was similar at about 20% of the cycle in all other species (Figure 3.2) perhaps suggesting a similar pattern of functional differentiation between A2 and A3 as *EMA* calculations. However, greater maxima of jaw power output seemed to appear relatively slower than lower maxima during the cycle. *Stenogobius hawaiiensis* exhibited the highest power output for both A2 and A3 (0.468 ± 0.207 W/kg/cm³ and 0.327 ± 0.166 W/kg/cm³, respectively: Table 3.8). *Lentipes concolor* appeared to produce the second highest maximum power in A2 and a similar level of power output in A3 as that seen in *S. hawaiiensis* (Table 3.8). *Sicyopterus stimpsoni*, *A. guamensis*, and *E. sandwicensis* all shared similar performance, with lower power output maxima in both A2 and A3 than in the other species (Table 3.8).

Species	Maximum Jaw Power A2/BL ³ (W/kg/cm ³)	Maximum Jaw Power A3/BL ³ (W/kg/cm ³)
<i>S. stimpsoni</i> (N=34)	0.198 ± 0.132, c	0.185 ± 0.132, b
<i>L. concolor</i> (N=23)	0.360 ± 0.199, b	0.338 ± 0.201, a
<i>A. guamensis</i> (N=19)	0.151 ± 0.122, c	0.160 ± 0.118, b
<i>S. hawaiiensis</i> (N=15)	0.468 ± 0.207, a	0.327 ± 0.165, a
<i>E. sandwicensis</i> (N=13)	0.141 ± 0.087, c	0.130 ± 0.088, b

Table 3.8: Maximum jaw power output of A2 and A3, normalized to body size. Values are means ± standard deviations. Species are grouped into a, b, and c ranks (a to c, in a decreasing manner) based on ANOVA ($F = 14.570$, $P < 0.0001$ for maximum jaw power output of A2, and $F = 7.916$, $P < 0.0001$ for maximum jaw power output of A3) and Fisher's LSD ($\alpha = 0.05$) post hoc test.

Morphological factors affecting simulation performance

Lever ratios for jaw closing based on skeletal measurements alone (i.e., skeletal mechanical advantage) strongly influenced output force, but the size of the adductor mandibulae muscles also played a major role (Tables 3.2 and 3.5). Relatively larger muscles can have relatively larger cross-sectional areas, enabling greater force production. For example, *E. sandwicensis* had the largest A2 and A3 at any given body size (Table 3.2), and accordingly this species exhibited the strongest bite force (Table 3.5). Similarly, A2 and A3 were both relatively large in one other species that also showed high bite forces (i.e., *A. guamensis*: Tables 3.2 and 3.5). However, muscle size is not the only factor that influences output force potential. For example, *S. hawaiiensis* showed a normalized output force of A2 nearly as high as that of *E. sandwicensis* and *A. guamensis*, but with its relatively smaller muscle mass this appeared to be largely due to its A2 having the highest mechanical advantage among the species considered (Table 3.4).

Comparing *L. concolor* and *A. guamensis*, differences in angular velocity between the two species (1.75 ± 0.53 °/ms and 2.46 ± 1.05 °/ms, respectively, $P = 0.0011$: Table 3.6) predicted by the simulation were not consistent with predictions based strictly on skeletal lever ratios, or measurement of *in vivo* feeding kinematics, that indicated similar jaw closing performance for these species (Chapter 2). In contrast, the high *EMA* of A2 in *S. hawaiiensis* is consistent with its high value of jaw closing lever ratio. However, *EMA* is a function not only of the skeletal jaw closing lever ratio, but also the angle of muscles onto each insertion point of the mandible (i.e., $EMA = MA \cdot \sin(\alpha)$; Westneat, 2003) as well as the ratio of output force to muscular force (i.e., $EMA = F_{out}/F_{act}$; Westneat, 2003). Therefore, the low *EMA* of both A2 and A3 in *A. guamensis* (Table 3.7) might be at least due to a low muscular insertion angle. In addition, differences in performance for all four functional variables between A2 and A3 seemed to have strong morphological association, further suggesting differentiation of the functional roles of the two muscle divisions. Greater muscle size in A2 can generate stronger bite forces, and longer muscle length in A3 (approximately 10% longer than A2: Table 3.3) can generate faster mandibular closure.

Discussion

Relationships between morphology and functional performance in the feeding systems of Hawaiian stream gobies

Our simulations of jaw closing in Hawaiian stream gobies indicate that several differences in functional performance among these species correlate well with

morphological differences between them. For example, the high output force of A2 and A3 in both *E. sandwicensis* and *A. guamensis* matches expectations from morphology because these muscles are significantly larger in these species than in the others measured in this study. However, other species exhibit alternative morphological strategies to achieve high relative output forces of both muscles. *Stenogobius hawaiiensis*, for instance, show normalized muscle forces almost as high as those of *E. sandwicensis* and *A. guamensis*, despite having smaller A2 and A3 masses. A major factor contributing to these high forces is the placement and configuration of the jaw muscles, reflected in the high mechanical advantage for A2 seen in *S. hawaiiensis* (Table 3.4). Thus, there are multiple anatomical pathways to reach similar functional performance in the feeding systems of Hawaiian gobioid fishes, reflecting the pattern of many-to-one mapping of morphology to performance cited by Alfaro et al. (2005) and Wainwright et al. (2005) for jaw function in labrid fishes, and by Blob et al. (2006) for climbing performance in several of these species of Hawaiian gobies.

Functional differentiation between A2 and A3 in Hawaiian stream gobioids

A2 function seems to emphasize force and A3 speed for all species. Possibly, fishes might activate these muscles differently to feed on different food items, helping to broaden their dietary repertoire and perhaps niches as well. In line with this possibility, it might be expected that a species with wider dietary breadth would show greater functional differentiation between A2 and A3. Conversely, we might have predicted less differentiation between A2 and A3 in *S. stimpsoni* because it has the most specialized diet and behavior. However, similar patterns of performance between A2 and A3 are seen in *S.*

stimpsoni as in the other species. Possibly *S. stimpsoni* has retained this pattern as a primitive state from their common ancestor with other gobies tested.

Some insights into ecology and evolution of Hawaiian gobioid species

Although our simulations show significant differences between species in several aspects of jaw closing performance, the distinctive feeding modes of several Hawaiian gobioid groups cannot be clearly associated with specific differences in performance variables. For instance, although *S. hawaiiensis* has significantly higher *A2 EMA* than other species, it is not clear why this would be advantageous for filter feeding of detritus. Moreover, several species with very different habitats share similar performance capacities. For instance, although only *E. sandwicensis* is a primary piscivore, its performance is very similar for almost all variables to that of *A. guamensis*. In addition, the high jaw power of the detritivore, *S. hawaiiensis*, is nearly matched by the power output of *L. concolor* (Table 8), which lives in fast flowing stream reaches and picks food out of the water column (personal observation). Thus, the diversity of feeding performance of Hawaiian stream gobioids does not show simple correlations with their habitats, but instead seems to reflect a combination of a maintenance of functional breadth with the retention of some primitive traits, in addition to novel functional capacities in several species.

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