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Feeding performance of king mackerel, *Scomberomorus cavalla*

Amber Rose Ferguson
University of South Florida, arf@mail.usf.edu

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Feeding Performance of King Mackerel, *Scomberomorus cavalla*.

by

Amber R. Ferguson

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Integrative Biology
College of Arts and Sciences
University of South Florida

Major Professor: Philip Motta, Ph.D.
Stephen Deban, Ph.D.
Daniel Huber, Ph.D.

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ABSTRACT

Although bite force is a commonly used metric of feeding performance, other factors such as bite pressure and strike speed are also likely to affect prey capture. Therefore, this study investigated static bite force, dynamic speeds, and predator and prey forces resulting from ram strikes, as well as bite pressure of the king mackerel, *Scomberomorus cavalla*, in order to examine their relative contributions to overall feeding performance. Theoretical posterior bite force ranged from 14.0-318.7 N. Ram speed, recorded with a rod and reel incorporated with a line counter and video camera, ranged from 3.3-15.8 BL/s. Impact forces on the prey ranged from 0.1-1.9N. Bite pressure, estimated using theoretical bite forces at three gape angles and tooth cross-sectional areas, ranged from 1.7-56.9 MPa. Mass-specific bite force for king mackerel is relatively low in comparison with other bony fishes and sharks, with relatively little impact force applied to the prey during the strike. This suggests that king mackerel rely on high velocity chases and high bite pressure generated via sharp, laterally compressed teeth to maximize feeding performance.

INTRODUCTION

Feeding performance, the ability to successfully capture and handle prey (Wainwright, 1988, 1991; Van Wassenberg et al., 2007; Habegger et al. 2010), is dependent upon a variety of sensory and musculoskeletal processes. Predators must first locate potential prey items using olfactory, visual, electrical, and hydrodynamic stimuli (Shashar et al., 2000; Pohlmann et al., 2001; Stewart et al., 2013), after which a successful strike must be initiated. Strikes may involve significant contribution of the locomotive system, as is the case in ram feeders such as the great barracuda, *Sphyraena barracuda*, which capture prey by striking at high velocity (Porter and Motta, 2004; Grubich et al., 2008). Alternatively, locomotion may make little contribution to the strike, as exemplified by suction feeders such as the sunfishes, family Centrarchidae, which generate negative pressures within the oropharyngeal cavity that draw water and prey items into the mouth (Lauder, 1980; Wainwright et al., 2001; Higham et al., 2005). Once prey is acquired, it generally must be processed within the oropharyngeal cavity via biting prior to deglutition (Huber et al., 2005; Grubich et al., 2008; Mara et al., 2009; Whitenack and Motta, 2010; Erickson et al., 2012). Thus, it is apparent that acquiring food involves the coordinated performance of sensory, locomotive, and feeding mechanisms. However, feeding studies have generally examined only individual performance parameters at a time. The simultaneous examination of multiple performance parameters will likely yield insight into the complex interaction between predator and prey (Rice and Westneat, 2005).

One of the more commonly assessed metrics of feeding performance is bite force, which is the emergent product of the morphology of the cranium and jaws, and physiology, architecture, and leverage of the jaw muscles (Herrel et al., 2001; Huber et al., 2005; Habegger et al., 2010). Bite force has been shown to affect resource partitioning and dietary diversity, with those species consuming hard prey having above average mass-specific bite forces (Wainwright, 1988; Herrel et al., 2001; Huber et al., 2005; Mara et al., 2009). Furthermore, ontogenetic studies have found that small and/or durophagous species exhibit positive allometry of bite force, which may allow those animals access to functionally difficult resources earlier in life than organisms with isometric ontogenetic trajectories (Kolmann and Huber, 2009; Habegger et al., 2012).

While significant relationships between morphology, behavior, and ecology have been found with regard to bite force, most of the studies on this topic have either focused on durophagous species (Hernandez and Motta, 1997; Huber et al., 2005; Kolmann and Huber, 2009), for which high bite forces are a prerequisite for the occupation of their ecological niche, or have neglected the role of the teeth in feeding performance (but see Herrel et al., 2001; Erickson et al., 2003, Erickson et al., 2012). Bite pressure, resulting from bite force applied over tooth contact area, is an often-neglected aspect of feeding performance that is complicated by a lack of knowledge regarding the number of teeth contacting the prey, how tooth contact area changes during tooth puncture, and how gape angle changes, consequently altering the bite force that drives tooth pressure (Whitenack and Motta, 2010; Gidmark et al., 2013). Some ram feeding fish such as the great barracuda, *Sphyrna barracuda*, have relatively low bite force (Habegger et al., 2010) but have very sharp teeth (Porter and Motta, 2004; Habegger et al., 2010). Consequently, the pressures generated by these teeth alleviate the need for high bite forces when feeding on soft-bodied prey. This relationship between tooth geometry and bite force is reversed

for durophagous species such as the horn shark, *Heterodontus francisci*, and striped burrfish, *Chilomycterus schoepfi*, which use high bite forces and molariform teeth to crush hard prey (Hernandez and Motta, 1997; Korff & Wainwright, 2004; Huber et al., 2005). Erickson et al. (2012) investigated the bite pressure generated by the caniform and molariform teeth of 23 species of extant crocodilians during prey capture and processing, and found higher bite pressures in piscivorous species with sharper teeth despite lower bite forces. Sharper and more pointed teeth may reduce the selection pressure for predators to develop high bite forces, with those species exhibiting rapid replacement of sharp teeth potentially exemplifying this relationship, (Wroe et al., 2008; Habegger et al., 2010; Whitenack et al., 2011). Thus, it is apparent that bite force does not tell the entire story with regard to feeding performance in ecological niches that have differing demands.

Like bite pressure, strike kinematics are another aspect of organismal performance that affects prey capture success, yet has received little attention in feeding studies (but see Norton, 1991; Porter and Motta, 2004). Many studies have examined fish swimming speeds (Bainbridge, 1959; Videler and Hess, 1984; McCormick and Molony, 1993; Bernal et al., 2001), yet the extent to which the impact generated during predator-prey contact affects the ability to disable prey is unknown. High velocity strikes such as those utilized by ram feeding fish transfer momentum to prey items, thereby accelerating them. The effect of the resultant force may contribute significantly to prey capture success, especially for sharp-toothed predators in which the impact may generate tooth pressures that cause puncture independent of the applied bite force. Because it is a dynamic interaction, when the predator strikes prey, such as small fish, only a fraction of the predator force is applied to the prey while the rest is applied to the environment. The

relationship between the force associated with the predator and that experience by the prey is affected by prey mass and forward momentum of the predator.

The purpose of this study was to examine the bite force, predator and prey impact force, and tooth pressure generated during feeding events in the ram-feeding king mackerel, *Scomberomorus cavalla* (Cuvier, 1828). King mackerel are coastal pelagic predatory fishes that are found along the Atlantic coast from North Carolina to Brazil, including the Gulf of Mexico. These fish have sharp, non-serrated, laterally compressed teeth (Morgan and King, 1983), suited for cutting soft-bodied prey (Wall et al., 2009). Top swimming speeds of king mackerel are unknown, but other mackerel species such as the Atlantic mackerel, *Scomber scombrus*, may attain burst speeds of up to 11 body lengths per second (bl/s) (Videler and Hess, 1984). In order to investigate the hypothesis that predator force and tooth pressure play an important role in the prey capture success of king mackerel, *Scomberomorus cavalla*, this study: (1) described the musculature used in generating bite force, (2) calculated maximal theoretical static bite force at three gape angles and the scaling relationships of bite force with respect to body length, (3) calculated the dynamic predator and prey forces that occur during predator-prey impact, and (4) estimated bite pressure exerted on the prey during tooth penetration. By examining bite force, predator force and tooth pressure, this study provides a more holist perspective on prey capture performance that has not been studied quantitatively to date.

MATERIALS AND METHODS

Specimen Collection for Theoretical Bite Force

King mackerel, *Scomberomorus cavalla* (Cuvier, 1828) were collected by hook and line in the Gulf of Mexico off Madeira Beach, Florida by recreational fishers. Fork length (FL), total length (TL), and weight were measured. Weight was estimated using a length-weight regression (SEDAR, 2009) when weight was unable to be directly determined. Heads were removed and frozen until dissections were performed (muscle nomenclature was based on Winterbottom, 1974).

Bite Force

Theoretical bite force was calculated for 23 fresh-frozen fish, sex undetermined, ranging from 63.2 cm to 117.8 cm FL, following the three-dimensional static equilibrium model used by Huber et al. (2005). Only force contributed by the lower jaw was considered, as the upper jaw is non-protrusible, and force contributed by the upper jaw would be a reaction to prey being driven into the upper jaw by the lower jaw. The adductor mandibulae divisions (A1, A2, A3) were modeled as a single muscle because of a common fiber direction, insertion, and line of action. The muscle was removed and bisected through its center of mass, perpendicular to its principal

fiber direction. To determine the center of mass the muscle was suspended from a string at two different points, and each time a line was traced along the string. Center of mass was the point where the two lines intersected. Photos of the cross sections were taken and anatomical cross sectional area (CSA) was measured using NIH Image J software (ImageJ64 v.1.42q, National Institute of Health, Bethesda, MD, USA). CSA was used instead of physiological cross sectional area due to the fibers being parallel (fiber angle $\sim 0^\circ$) near the insertion of the muscle. Near the origin of the muscle, the fibers diverged from parallel and changed to accommodate the eye dorsally, however this was not included in the model as fibers were approximately parallel at the center of mass. Position of the origin and insertion of the adductor mandibulae complex, anterior and posterior bite points (dorsal surface of the mandibular symphysis and last tooth near the jaw joint, respectively), and jaw joint were obtained using a three-dimensional digitizer (Polhemus, Colchester, VT, USA). The maximum theoretical tetanic output (P_0) of the adductor musculature was calculated by multiplying CSA by the specific tension (T_s) of fish muscle (25 Ncm^{-2} ; Herrel et al., 2002).

$$P_0 = CSA * T_s$$

Anterior and posterior bite forces (ABF and PBF respectively) were modeled via a 3D static equilibrium analysis in Mathcad (11.1, Mathsoft, Inc., Cambridge, MA, USA), and bite force was calculated with the following equation:

$$\sum F_{LJ} = F_{JR} + F_{AM} + F_B = 0$$

Where F_{LJ} is the force on the lower jaw, F_{JR} is the jaw joint reaction force, F_{AM} is the force generated by the adductor musculature, and F_B is the bite reaction force of the prey.

Theoretical bite force was calculated with the jaw closed (0% maximum gape), half open (50% maximum gape), and maximally open (100% maximum gape) (Fig. 1). Mechanical

advantage (MA) was calculated for all individuals at the three gape angles for both anterior and posterior bite positions. MA is the ratio of the force in-lever (distance from the muscle insertion to the jaw joint) divided by the force out-lever (distance from the bite point to the jaw joint).

Electrically stimulated tetanic bite force values were measured on a subset of six fish to validate theoretical estimates. Fish were caught using a rod and reel with an analog line counter (Diawa Saltist STTLW50LCA, Cypress, CA, USA) and a mounted GoPro Hero 2 or GoPro Hero 3 HD camera (120 fps and 240 fps, respectively) focused on the line counter. Lines were baited with frozen-thawed Spanish sardines, *Sardinella aurita*, live blue runner, *Caranx crysos*, or live mackerel scad, *Decapterus macarellus*. Fish were caught and immediately euthanized with an overdose of a 0.2% tricaine methanesulfate (MS 222) solution buffered with sodium bicarbonate by spraying the solution onto the gills. The adductor mandibulae (bilateral) divisions were stimulated for approximately two seconds (30V, 60Hz, 0.02ms delay, 3ms pulse length) with a SD9 stimulator (Grass Telefactor, Quincy, MA, USA) by implanting stainless steel hypodermic needles ~2.5 cm apart through each cheek into the adductor mandibulae complex. A piezoelectric load cell with custom lever arms (PCB Piezotronics 201BO2) was placed between the anterior teeth (approximately 30% maximum gape) during stimulation of the anesthetized fish. Data were acquired with a 6020E data acquisition board and LabVIEW 6.0 software (National Instruments Corp., Austin, TX, USA). This procedure was repeated 2-3 times per individual, with 1-3 minutes of rest between trials, and the largest value was recorded as maximal bite force.

Predator and Prey Forces and Predator Speed

Seven king mackerel were caught as above (see Bite Force), using braided fishing line (Power Pro Depth Hunter 30lb) to minimize stretching and reel drag set as low as possible so as to not limit strike speed of the fish or cause the line to free spool or tangle. Boat speed at the time of capture was recorded with a GPS (Magellan Explorist 210, Santa Clara, CA, USA) and subsequently subtracted from strike speed (see below). A strike was measured when a king mackerel struck a baitfish and swam away from the boat. Videos of the line counter were digitized using GoPro Cineform Studio Version 1.2 to quantify the distance travelled by the line throughout the strike per unit time. These data were in turn fitted with an n th (5, 6, or 7) order polynomial that was numerically derived to ascertain line velocity and acceleration. The order of the polynomial was chosen for best fit by Student's paired t-test comparing data points from the digitized GoPro video (distance by time plot) and the same points from the calculated polynomial curves. The best fit curve had the lowest t value. The velocity and acceleration of the fishing line was assumed to be the same as the prey fish and the hooked king mackerel, and was used as a proxy for potential strike speed when the predator hit the prey. As the hook was attached to the prey during capture, the initial maximal acceleration measured is the acceleration of the predator and prey immediately after the impact occurred.

The amount of force required to stop the king mackerel from forward acceleration is equivalent to the maximum force the king mackerel is capable of exerting on the environment. This predator force was calculated as the negative of the mass of the predator, multiplied by the acceleration of the predator and prey fish throughout the strike:

$$F_{Pd} = -(m_k * a_k)$$

where F_{Pd} is the predator force the king mackerel is capable of exerting on the environment during forward motion, m_k is the mass of the king mackerel, and a_k is the acceleration of the king mackerel and captured prey from the strike until it reached a maximum velocity

It is evident that not all available forward force was applied to the prey during capture. Prey force, the amount of force applied to the prey during forward acceleration of the prey, was estimated using Newton's second law of motion:

$$F_{Py} = m_{py} * a_{py}$$

where F_{Py} is the predator force, m_{py} is the mass of the prey and a_{py} is the acceleration of the prey.

Predator and prey forces were calculated assuming that the motion of the king mackerel toward the prey item was only in one plane, that the prey is motionless at the time of impact, and that the fishing line does not stretch. Skin friction drag on the fishing line was determined by trailing three lengths of line (30, 45, and 60 m) from a Rapala digital scale (RGSDS-50, Finland) behind the boat moving at an average trolling speed of 0.9 m/s. The forces created by drag on the fishing line alone were 0.3N, 0.3N, and 0.6N for lengths of line at 30, 45, and 60m, respectively.

Bite Pressure

Bite pressure was calculated using teeth from the lower jaws of three fish (small: FL=70cm; medium: FL=88cm; large: FL=107cm). Bite pressure was calculated assuming that four teeth from each half of the lower jaw (8 teeth total) contact the prey at the same time during biting, based on the observation of failed prey captures on Spanish sardines (Fig. 2). Only lower

jaw teeth were considered, as this was assumed to be a static system in which the upper jaw and lower jaw would be mirror images of force and pressure production. Pressure was measured from the most anterior teeth to the most posterior teeth in consecutive increments of four teeth (e.g., 1 to 4, 2 to 5, etc.). Following this, all teeth were separated at their bases using a Dremel tool and indented orthogonally into modeling clay at 10%, 50% and 100% of crown height to correspond with bite forces calculated for 100%, 50% and 0% of max gape, respectively. A minimum distance of 10% penetration was chosen to represent the tooth tip because measurement of cross-sectional area of the exact tooth tip is imprecise (Erickson et al., 2012). Consequently, puncture pressure of the tooth tip is an underestimate. Depth of tooth penetration determined which gape angle value of theoretical bite force was used (10% penetration = 100% Maximum gape; 50% penetration = 50% maximum gape; 100% penetration = 0% maximum gape). The maximally open position of the jaw was used in the calculations for maximum bite pressure as the observation of failed strikes on Spanish sardines suggests the king mackerel strike the prey with the mouth fully open. This was evidenced by tooth puncture spacing on that of the recovered prey that matched that of the most posterior teeth of the king mackerel (Fig 3.). Consequently, anterior bite pressure values were conservative, as the jaw would, in reality, be less than 100% maximally open when the tips of the teeth penetrate (see Results). Photos of the tooth indentations in the clay were taken, and the cross sectional area was measured using NIH Image J software (ImageJ64 v.1.42q, National Institute of Health, Bethesda, MD, USA). Theoretical bite force was calculated along the length of the lower jaw (as above), after which the theoretical bite force corresponding to tooth depth was averaged over the four penetrating teeth and divided by the cross sectional areas of the penetrating teeth to obtain the penetration pressure of the four teeth (Fig. 2).

All experimental procedures were approved by the Institutional Animal Care and Use Committee (IACUC) protocols W IS00000002 and T IS00000021 of the University of South Florida.

Statistical Analysis

Data was tested for normality using the Shapiro Wilk test, and homoscedasticity using the Bartlett test. Student's paired T-test was used to compare stimulated and calculated theoretical anterior bite force values for the same six individuals. Scaling of theoretical bite force was analyzed at all three gape angles and at both the anterior and posterior bite points for the available size range of fish. Theoretical bite force, jaw muscle cross sectional area, and mechanical advantage were log transformed and linear regressed using least-squares regression against log fork length for the three different gape angles in order to assess scaling relationships of bite force. Least squares regression was used as the error in the dependent variable is expected to be much higher than the error in the independent variable. 95% confidence intervals were compared to the isometric slope of 2 to determine allometric relationships of bite force and adductor CSA to body length and an isometric slope of 0 for mechanical advantage. A comparison was not made between prey, predator and stimulated bite force due to a lack of individuals with both sets of data available. Bite force was linearly regressed against gape angle to determine if bite force changes with gape angle. In order to compare the maximal anterior bite force of *Scomberomorus cavalla* to that of 19 other fish species, $\log_{10}$ anterior bite forces were linearly regressed using least-squares regression against $\log_{10}$ fish mass and studentized residuals were compared. Bite pressure was linearly regressed using least-squares regression against

distance along the jaw and indentation depth. Each regression was tested for significance using Analysis of Variance (ANOVA). All analyses were performed using R statistical software (R Foundation for Statistical Computing, Vienna, Austria).

Fig. 1. Absolute values of calculated Log theoretical bite force (N) at (A) 0% maximum gape or mouth closed ($\text{LogABF}=3.0\text{XLogFL}-4.5$; $\text{LogPBF}=2.8\text{XLogFL}-3.5$), (B) 50% maximum gape or mouth half open ($\text{LogABF}=2.1\text{XLogFL}-2.8$; $\text{LogPBF}=2.0\text{XLogFL}-2.1$) and (C) 100% maximum gape, mouth fully open ($\text{LogABF}=3.1\text{XLogFL}-4.9$; $\text{LogPBF}=3.1\text{XLogFL}-4.3$). Closed circles represent anterior bite force (ABF) and open circles represent posterior bite force (PBF).

Fig. 2. Diagram of prey being bitten by a king mackerel, *Scomberomorus cavalla*. Teeth in contact with the prey were used for calculation of bite pressure. Calculations were made from anterior to posterior teeth for four consecutive teeth; this diagram depicts a representative position with the prey at a middle position along the lower jaw with the tooth tips contacting it.

Fig 3. The spacing of the two lines cut by the teeth on (A) recovered prey from a failed strike matches those made by (B) a simulated strike on a similarly sized prey in the laboratory using the teeth of a king mackerel of the same size. Anterior teeth would result in two lines that are closer together.

RESULTS

Anatomy

The adductor mandibulae of king mackerel is made up of the A1, A2, A3, and Aw subdivisions (Fig. 4). The most superficial subdivisions, A1 and A2, make up a fan shaped muscle complex originating on the pterotic, frontal and preopercular bones. The A1-A2 complex inserts via a tendinous sheath extending from the maxilla to the Meckelian fossa and articular. Deep to the A1-A2 complex, the A3 subdivision is parallel fibered and originates on the hyomandibula, metapterygoid, quadrate, and preopercle (Fig.4). The tendons of the A1-A2 complex and A3 subdivision fuse into a single tendon, that inserts into the Meckelian fossa and on the articular. The Aw subdivision is a bipennate muscle that lies within the Meckelian fossa on the medial face of the dentary, inserting on the medial side of the quadrate and preopercle, and originating on the dentary and articular.

Bite Force

Anterior mechanical advantage (MA) was 0.18 ± 0.04 , 0.20 ± 0.05 , and 0.21 ± 0.06 at 0%, 50%, and 100% maximum gape respectively, while posterior mechanical advantage was 0.62 ± 0.13 , 0.77 ± 0.25 , and 0.71 ± 0.25 at these gapes respectively. Theoretical anterior bite

force ranged from 5.1-70.5N at 0% maximum gape, 3.8-53.6N at 50%, and 5.9-33.3N at 100%. Posterior bite force ranged from 27.3-318.7N at 0% maximum gape, 25.5-153.1N at 50%, and 14.0-154.2N at 100% gape (Table 1). Bite forces were inversely proportional to gape angle ($P < 0.001$, Fig 5.), with average bite force highest at 0% maximum gape (anterior = $22.9 \text{ N} \pm 14.2 \text{ SD}$, posterior $110.1 \text{ N} \pm 64.0 \text{ SD}$), decreasing at 50% maximum gape (anterior = $17.0 \text{ N} \pm 7.7 \text{ SD}$, posterior = $68.4 \text{ N} \pm 31.5 \text{ SD}$), and being lowest at 100% maximum gape (anterior = $16.5 \text{ N} \pm 11.9 \text{ SD}$, posterior = $55.7 \text{ N} \pm 36.3 \text{ SD}$) Bite force scaled isometrically with respect to body size at all three gape angles (Fig. 1). Cross sectional area of the adductor mandibulae complex scaled with positive allometry ($b=2.4$, 95%CI 2.1-2.7). Mechanical advantage scaled isometrically at 0% (anterior $b=0.2$, 95%CI -0.4-0.6; posterior $b=0.2$, 95%CI -0.4-0.8), 50% (anterior $b=-0.1$, 95%CI -0.7-0.3; posterior $b=-0.1$ 95%CI -0.8-0.5), and 100% maximal gape (anterior $b=0.2$, 95%CI -0.6-0.9; posterior $b=0.0$, 95%CI -0.7-0.8).

Stimulated bite force for six individuals (taken with the mouth approximately 30% maximum gape) were not significantly different ($P > 0.05$) from theoretical bite force values taken at the anterior bite point for the same individuals at 0% and 50% maximal gape, but was larger than bite force estimated at 100% maximal gape (Fig. 6).

Predator and Prey Forces and Predator Speed

Maximum velocity of the king mackerel ranged from 3.3-15.8 bl/s and maximum initial accelerations of the prey ranged from 0.5 to 12.8 m/s^2 (Table 2). Force applied to the prey ranged from 0.1 to 1.9N while maximum predator force of the king mackerel ranged from 2.1 to 81.6N (Table 2).

Bite pressure

Jaw position had a significant effect ($P < 0.05$) on bite pressure in the smallest and largest fish, with higher pressures toward the back of the jaw. Maximum bite pressures were 18.1MPa, 25.2MPa and 56.9MPa for the small, medium and large fish, respectively. Tooth depth had a significant effect ($P < 0.001$) on bite pressure for all three fish, with higher pressure when 10% (tip) of the tooth was penetrated and lower pressure at 50% and the lowest pressure at 100% (Fig 7., Table 3).

Comparison Among Other Fishes

There was a significant positive relationship between bite force and mass for 20 species of teleost fishes and sharks ($\text{Log ABF} = 0.507 \log \text{mass} + 0.317$, $r^2 = 0.565$, $P < 0.001$). King mackerel had the second lowest mass specific bite force (Table 4).

Fig. 4. Jaw closing musculature of the king mackerel, *Scomberomorus cavalla*. The lacrimal bone is not shown. (A) The Adductor mandibulae 1 and 2 (A1 + A2) muscle is the most superficial fan shaped muscle. Red circles represent points digitized in 3D space for calculation of theoretical bite force. Lower jaw angle is the obtuse angle between the two red lines, representing the line of action of the muscle and the length of the lower jaw. (B) The adductor mandibulae 3 (A3) is deep to the A1A2 complex and overlaps the levator arcus palatini (LAP) muscle.

Fig. 5. Bite force of king mackerel, *Scomberomorus cavalla*, at different gapes. Circles represent the average bite force in Newtons (N) at the three different gape angles, 0% (mouth closed), 50% (mouth half open) and 100% (mouth fully open) maximum gape. Closed circles represent anterior bite force values and open circles represent posterior bite force values. Error bars are one standard deviation from the average.

Fig. 6. Bite force values of six king mackerel, *Scomberomorus cavalla*, measured using stimulated bite force and calculated theoretical anterior bite force for the same individuals at 0% maximal gape (mouth closed), 50% maximum gape (mouth half open), and 100% maximal gape (mouth maximally open). Stimulated measured bite force (at approximately 30% maximum gape) was not significantly different than estimated theoretical bite force at 0% maximum gape ($P>0.05$) and 50% maximum gape ($P>0.05$), but greater than estimated theoretical bite force at 100% maximal gape ($P<0.05$). Each individual is represented by one of the six symbols.

Fig. 7. Bite pressure as a result of tooth indentation, depth, and position of prey along the jaw for a small (A) (FL=70cm, 2.6kg), medium (B) (FL=88cm, 5.3kg), and large (C) (FL=107cm, 9.5kg) king mackerel, *Scomberomorus cavalla*. Tooth depth refers to the depth at which the tooth was indented into the clay. Teeth were indented at the tip of the tooth (10% of crown height), half of the tooth (50% of crown height), and the entire tooth (100% of crown height) representing 0%, 50%, and 100% mouth closure. Jaw position refers to the position of the prey along the lower jaw. The most anterior tooth was assigned the position 0.0 and the most posterior tooth was assigned the position 1.0.

Table 1. Absolute values of bite force for 23 individual king mackerel, *Scomberomorus cavalla*. Fork length is expressed in centimeters (cm). Bite force values are expressed in Newtons (N). Anterior refers to bite force estimated at the anterior bite point, and posterior refers to bite force estimated at the posterior bite point. At each bite point bite force was calculated at three different gape angles, 0% maximum gape (mouth closed), 50% maximum gape (mouth half open), and 100% maximum gape (mouth maximally open).

FL (cm)	Anterior			Posterior		
	0%	50%	100%	0%	50%	100%
63.2	11.4	8.0	9.2	53.1	36.6	23.3
69.6	9.7	5.1	10.9	50.8	33.4	18.9
72.8	13.5	15.6	11.9	70.6	58.9	53.7
76.5	21.0	10.5	11.0	100.7	44.4	34.8
79.1	19.4	14.2	20.6	95.1	96.4	44.8
79.4	5.6	5.7	8.6	31.4	41.6	20.8
80.9	14.1	8.5	8.3	93.4	39.5	40.4
81.2	5.1	3.8	5.9	27.3	25.5	14.0
84.0	19.7	15.8	19.6	93.9	66.7	50.1
84.9	30.4	16.0	21.2	137.7	84.2	53.0
86.0	16.8	7.8	14.2	77.8	55.6	27.3
86.9	19.1	17.9	15.1	92.9	65.2	58.8
87.0	17.3	10.2	12.4	90.9	51.9	39.4
88.0	17.7	13.7	17.9	76.7	66.6	45.4
89.2	20.2	17.7	16.9	85.0	59.5	57.9
90.0	28.3	13.7	21.3	136.4	85.4	54.1
92.9	23.1	17.0	24.2	111.6	96.0	57.6
93.8	27.8	18.6	15.6	132.3	55.9	51.8
98.6	19.6	9.7	11.6	98.7	48.7	30.9
104.0	32.9	43.6	35.2	154.0	153.1	122.6
107.0	39.2	22.0	25.4	193.8	92.4	122.6
114.2	70.5	30.8	21.3	318.7	81.6	104.4
117.8	44.6	53.6	33.3	209.8	134.8	154.2

Table 2. Results obtained from rod and reel strike trials for seven king mackerel, *Scomberomorus cavalla*. Mass of each fish is expressed in kilograms (kg), the table is ordered by increasing mass. Fork length (FL) of each fish is expressed in centimeters (cm). Maximum velocity for each fish is expressed in body lengths per second (bl/s). Maximum acceleration of each fish is expressed in m/s^2 . Prey force is the force actually exerted on the prey, and is expressed in Newtons (N). Predator force is the maximum force the king mackerel is capable of exerting on the environment in the forward direction and is expressed in Newtons (N).

Mass (kg)	FL (cm)	Max velocity (bl/s)	Max acceleration (m/s^2)	Prey force (N)	Predator force (N)
3.4	76.5	13.6	11.5	1.7	39.7
3.8	79.1	5.0	1.4	0.2	5.5
3.9	79.4	9.4	9.1	1.4	35.0
4.1	81.9	3.3	0.5	0.1	2.1
4.1	81.2	15.8	7.6	1.1	31.4
4.3	82.0	8.8	12.8	1.9	54.6
7.4	98.6	3.7	11.0	1.7	81.6

Table 3. Bite pressure (MPa) values of a small (FL=70cm, 2.6kg), medium (FL=88cm, 5.3kg), and large (FL=107cm, 9.5kg) king mackerel, *Scomberomorus cavalla*. Jaw position refers to the position of the prey along the lower jaw. The most anterior tooth was assigned the position 0.0 and the most posterior tooth was assigned the position 1.0. The number of measurement increments of four consecutive teeth per fish determined the number of jaw positions, thus there are more position in the larger fish. Larger fish have more tooth positions because of a larger total number of teeth along the lower jaw. Bite pressure values are reported in MPa for tooth penetration values of 10% (tip of tooth penetrating), 50% (half of tooth penetrating), and 100% (whole tooth penetrating) of tooth crown height.

Small				Medium				Large			
Jaw position	10%	50%	100%	Jaw position	10%	50%	100%	Jaw position	10%	50%	100%
1.00	17.4	5.3	4.9	1.00	23.6	6.6	3.3	1.00	56.9	5.1	5.2
0.90	16.4	4.7	4.1	0.92	20.2	5.4	2.8	0.93	44.9	4.5	4.5
0.80	15.4	3.8	3.4	0.83	19.2	4.7	2.6	0.86	42.5	4.4	4.2
0.70	18.1	3.6	3.1	0.75	18.2	4.1	2.4	0.79	40.0	3.8	3.8
0.60	16.8	3.2	2.6	0.67	22.2	5.1	3.0	0.71	41.0	3.8	3.7
0.50	15.6	3.2	2.4	0.58	23.5	4.9	2.9	0.64	38.3	3.5	3.7
0.40	14.4	3.4	2.2	0.50	25.2	4.6	2.8	0.57	32.6	3.4	3.6
0.30	13.2	3.0	1.8	0.42	19.7	4.8	2.7	0.50	30.1	3.6	3.8
0.20	11.9	2.8	1.7	0.33	16.6	3.8	2.1	0.43	30.2	3.6	3.8
0.10	10.7	2.8	1.7	0.25	15.4	3.7	2.0	0.36	27.5	3.6	3.7
0.00	9.5	2.8	1.8	0.17	14.1	3.8	2.0	0.29	27.3	3.6	3.8
				0.08	17.2	4.1	2.2	0.21	27.0	3.6	3.6
				0.00	15.5	4.3	2.2	0.14	23.8	4.0	4.0
								0.07	20.5	4.6	4.2
								0.00	19.3	4.6	4.2

Table 4. Values of anterior bite force (ABF) for 20 species of teleost and cartilaginous fishes obtained from the literature. Studentized residuals are from a linear regression of log ABF against log mass.

Species name	Common name	ABF(N)	Mass(g)	Residuals
<i>Chilomycterus schoepfi</i> ^a	striped burrfish	380	180	2.086
<i>Lachnolaimus maximus</i> ^b	hogfish	290	209	1.747
<i>Archosargus probatocephalus</i> ^c	sheepshead	309	998	1.114
<i>Heptranchis perlo</i> ^d	sharpnose sevengill shark	245	1614	0.747
<i>Heterodontus francisci</i> ^e	horn shark	206	2948	0.394
<i>Hydrolagus collieri</i> ^f	whitespot chimaera	106	870	0.359
<i>Sphyrna mokarran</i> ^g	great hammerhead shark	2432	580598	0.277
<i>Carcharhinus limbatus</i> ^h	blacktip shark	423	22092	0.18
<i>Halichoeres maculipinna</i> ^b	clown wrasse	11	18	0.152
<i>Carcharhinus leucas</i> ^g	bull shark	1023	140341	0.146
<i>Chiloscyllium plagiosum</i> ^d	whitespotted bambooshark	93	1219	0.142
<i>Negaprion brevirostris</i> ^d	lemon shark	79	1219	0.025
<i>Halichoeres garnoti</i> ^b	yellow head wrasse	10	21	0.022
<i>Thalassoma bifasciatum</i> ^b	bluehead wrasse	5	7	-0.083
<i>Halichoeres bivittatus</i> ^b	slippery dick	5	19	-0.464
<i>Sphyrna barracuda</i> ⁱ	great barracuda	83	11900	-0.799
<i>Squalus acanthias</i> ^j	piked dogfish	19.6	1065	-0.95
<i>Etmopterus lucifer</i> ^d	blackbelly lanternshark	3.1	48	-1.197
<i>Scomberomorus cavalla</i>	king mackerel	44.58	12684	-1.33
<i>Etmopterus spinax</i> ^d	velvet belly lanternshark	1.6	349.1	-2.81

^aKorff & Wainwright (2004).

^bClifton & Motta (1998).

^cHernandez & Motta (1997).

^dHuber (2006).

^eHuber et al. (2005).

^fHuber et al. (2008).

^gHuber & Mara (unpubl. data).

^hHuber et al. (2006).

ⁱHabegger et al. (2010).

^jHuber & Motta (2004).

DISCUSSION

Bite Force

A better understanding of feeding performance is likely to be gained by simultaneously considering multiple performance parameters during feeding events. The results of this study indicate that king mackerel generate relatively low biting and prey forces while striking at high velocities with high tooth pressures. King mackerel have an intermediate mechanical advantage (MA) (Westneat, 2004) at the anterior (0.18-0.21) bite point resulting in a speed-efficient jaw with an inefficient transfer of force from the muscle to the jaw. Mechanical advantage at the posterior (0.62-0.77) bite point resulted in a more efficient transmission of force than at the anterior bite point. Variation in the posterior MA may be due to error during digitizing of the posterior bite point, as the last tooth position was variable and difficult to ascertain. Most piscivorous fish rely on speed efficient jaws (low MA) rather than force efficient jaws (high MA) in order to capture elusive prey (Westneat, 2004). The great barracuda, *Sphyraena barracuda*, which consumes similar prey to the king mackerel, has an average anterior MA of 0.27 (Habegger et al., 2010). However the durophagous horn shark, *Heterodontus francisci*, has an anterior MA of 0.50 and posterior MA of 1.06, in which the resultant bite force exceeds the force generated by the adductive musculature (Huber et al., 2005). Mechanical advantage of the jaw in-lever and out lever showed no allometry with respect to predator length at any gape angle.

Compared with 19 species of sharks and teleost fish studied to date, king mackerel had the second lowest anterior mass-specific bite force (Table 4), with only the velvetbelly lanternshark, *Etmopterus spinax*, producing a lower mass-specific bite force (Huber et al., 2009). Bite force of king mackerel scaled isometrically with respect to body size for adult king mackerel (Fig. 1). By contrast, the bite force of the bull shark, *Carcharhinus leucas*, scaled with positive allometry for juveniles and with isometry for adults (Habegger et al., 2012). The pattern exemplified by the bull shark suggests that it may be important for juveniles to rapidly develop high bite forces in order to exploit prey resources, but that the large size and absolute bite forces of adults alleviates the need for allometric performance. More work is needed to examine if there exists a different scaling relationship between juvenile and adult king mackerel as all mackerel in this study were adults. Despite isometry in bite force, the CSA of the adductor mandibulae complex scaled with positive allometry. This apparent discrepancy may be due large variability in the MA that masks the positive allometry seen in the CSA of the adductor complex, resulting in isometry of bite force values.

Stimulated bite force (taken at the anterior jaw), at approximately 30% of maximum gape, did not differ significantly ($P=0.056$) from the theoretical anterior bite force estimated at 0% and 50% maximum gape, suggesting that the 3D-static equilibrium model for estimating bite force is representative of actual tetanic bite force for this species. Stimulated bite force was larger than theoretical bite force at 100% maximal gape because the theoretical bite force was the lowest when the gape was maximally open. However, the marginal significance value indicates a possible difference, with the stimulated values being greater than the theoretical bite force that might be seen by examining a larger sample size. A similar relationship between modeled and stimulated bite force was seen in the durophagous bonnethead shark, *Sphyrna tiburo*, where the

anterior (20.0N) and posterior (77.4N) theoretical bite forces did not differ from the stimulated anterior (17.3N) and posterior (64.6N) bite forces (Mara et al., 2009).

Bite force measured simply as a maximum value ignores the length-tension relationships of muscles, insertion angles of tendons, and changes in the jaw lever system. Thus, bite force is affected by gape angle, with numerous studies having found maximum bite forces at intermediate gape angles (Williams et al., 2009; Christiansen, 2011, Gidmark et al., 2013). For example, Williams et al. (2009) found that the bite force of rodents peaked at approximately 40% of maximum gape and Ferrara et al. (2011) found that white sharks, *Carcharodon carcharias*, have higher bite forces at a gape angle of 35° (mouth open, 1602N) than 0° (mouth closed, 1303N) because a unique attribute of the primary jaw adductor (mid-lateral raphe) allows reorientation of muscle fibers during mouth opening. Unlike these studies, king mackerel bite force was inversely proportional to gape angle, which has also been observed among bat species (Dumont et al., 2003). As bite force is relatively low in king mackerel it is possible they rely on consumption of small prey and other parameters and have no need to abide by the patterns seen in other large predators that must accommodate large prey.

The limited amount of volume within the vertebrate head may result in an evolutionary compromise, such as spatial trade-offs on adjacent body structures or size of the constituent parts (Hulsey et al., 2007). In some cichlids (Cichlidae) the suspensorium and adductor muscles may be reduced by large eye size (Barel, 1983, Hulsey et al., 2007). In the case of king mackerel, low bite force may be a result of a hydrodynamic trade off in that streamlining of the body selects against large jaw adductor muscles, thereby constraining bite force (Herrel et al., 2001; Herrel et al., 2002). Boundary layer separation can be delayed, resulting in reduced pressure drag when the widest plane of the fish is further back on the body (Walters, 1962). The widest plane of the king

mackerel occurs near the operculum, just posterior to the jaw adductors. Thus, having higher biting forces and the necessary large jaw adductor muscles (Herrel et al., 2001) could hinder swimming performance of king mackerel, thereby compromising the speed of their strike. In the bull shark, *Carcharhinus leucas*, head width is positively correlated to bite force, and this shark generates the highest mass specific bite force of any shark measured to date (Habegger et al., 2012). Therefore, it seems that large ram-feeding predators occupy this niche by virtue of selection for disparate parameters.

Predator and Prey Forces and Predator Speed

King mackerel attain high strike velocities (15.8 m/s, Table 2) resulting in forward forces being exerted on their prey during feeding. Forces on prey (1.9N, Table 2) were lower than static biting forces of king mackerel. Because of the relative masses of the king mackerel and the smaller prey fish, only a small fraction of the predator force is actually applied to the prey item, where a larger prey item would experience a larger fraction of the predator force. Although the forces on the prey resulting from high-speed attacks are small, high speeds may be important for surprising and chasing down elusive prey. Walters (1962) estimated a conservative swimming speed of scombroid fishes to be approximately 10 bl/s, with other studies documenting peak swimming speeds of 13.4 bl/s in the bluefin tuna, *Thunnus thynnus*, and 11.0bl/s in the Atlantic mackerel, *Scomber scombrus* (Lane, 1941; Videler and Hess, 1984). Aquarium-housed juvenile great barracuda were reported to strike prey at 7.5 bl/s, although this was likely submaximal performance (Porter and Motta, 2004). Similar to other scombroids, king mackerel benefit from high swimming speeds in their ability to successfully chase down and capture elusive prey.

Regardless of low forces on the prey during the strike, shark teeth have been determined to puncture teleost fishes with forces as low as 1.1N (Whitenack and Motta, 2010).

Bite Pressure

The generation of high bite pressures facilitates the consumption of soft-bodied prey and likely alleviates any perceived performance deficiency attributed to low bite or prey forces. For example, the sharp teeth of sharks require very little force to penetrate prey such as ladyfish, *Elops saurus* (mean 6.7 ± 1.3 N), and white grunt, *Haemulon plumieri* (mean 10.9 ± 2.1 N) owing to high pressures generated during biting (Whitenack and Motta, 2010). King mackerel are able to produce bite pressures upwards of 57MPa (Fig. 7, Table 3), which is consistent with other piscivorous vertebrates. In fact, piscivorous crocodilian with low bite forces are capable of generating bite pressures of upwards of 1344 MPa (Anderson and Westneat, 2006; Erickson et al., 2012). The bite pressure of king mackerel was highest at the posterior jaw when only the tip of the tooth was penetrating the prey (Fig. 7) and decreased greatly as tooth penetration depth increased. As bite pressure is greatest posteriorly, while tooth size increases posteriorly and worn teeth are readily replaced to maintain a sharp cutting surface (Morgan and King, 1983), it may be advantageous to strike and/or bite prey at this posterior region. This finding is consistent with the observation of bite marks from failed captures on bait. The gape must be at a large angle in order for prey to reach the rear of the mouth, a jaw position that results in lower bite force, suggesting again that bite pressure may play a more important role in feeding than absolute bite force.

It is unknown whether or not prey contact due to jaw closure, and forward motion of the predator, occurs at the same instant. If these two events are instantaneous, the resultant forces on

the prey may be additive. Because the prey size is small relative to the king mackerel the predator force would contribute little to overall feeding success allowing biting forces to dominate. High-speed kinematic studies of striking great barracuda (Porter and Motta, 2004) suggest that it is likely these two events occur at the same time, although kinematic analyses of king mackerel feedings are needed to elucidate this relationship.

Conclusions

King mackerel, *Scomberomorus cavalla*, have a relatively low performance for bite force compared with other fishes and relatively little of the forward predator force is experienced by the prey. However, king mackerel can attain high swimming speeds to chase prey and use sharp teeth to impart high bite pressure, factors which apparently alleviate the need for high bite forces.

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