

Bite Force in American Monkfish

by

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ABSTRACT

This study examined bite force generation in American monkfish (*Lophius americanus*) and how it scaled with size, focusing in particular on the roles of the quadrato-mandibularis (QM) muscle and mechanical advantage in jaw closure in this species. Considering the feeding strategy of other anglerfishes, it was hypothesized that monkfish would trend towards force optimization rather than speed optimization in terms of the jaw closing system. The data revealed that bite force has a slightly positive allometric scaling relationship with size, while mechanical advantage was constant throughout growth. Maximum theoretical bite force ranged from 8 N to 87 N, with total lengths ranging from 17 cm to 51 cm. When comparing the bite force of the American monkfish to that of 10 other fish species, small monkfish exhibit a bite comparable to similarly sized species. However, larger monkfish were estimated to have a stronger bite than organisms of similar size.

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CHAPTER ONE

Introduction

Bite force is a measure of feeding performance that quantifies the strength of an organism's bite (Habegger et al., 2012; Van der Meijden et al., 2023). Bite force is an important aspect of an organism's biology as it directly influences feeding strategies related to capturing and consuming prey, which is strongly linked to fitness (Gu and Xie, 2021; Herrel and O'Reilly, 2006). Body size and cranial morphology are strongly correlated with bite force, meaning that in vertebrates, such studies can provide insight into prey capture abilities, further connecting the link between fitness and morphology (Herrel and O'Reilly, 2006; Kim et al., 2018). An organism that tends to eat larger and harder prey may bite harder, making bite force a performance trait that has ecological relevance (Goswami, 2011; Meers, 2002).

Bite force estimates should follow the Ecomorphological Paradigm, which states that organismal form should relate to function (Leim, 1993). In other words, an organism's ecological role within a community or ecosystem should be evident from, at least in part, its morphological traits (Motta et al., 1995). In the context of bite force estimation, the paradigm suggests that jaw anatomy, arrangement of jaw muscles, body size, and teeth shape have evolved to optimize bite force biomechanics based on the demands of the environment (Leim, 1993; Motta et al., 1995; Wainwright, 1994). These features can be quantified to estimate bite force for various applications using principles of basic Newtonian physics (Mara et al., 2010; Shi et al., 2020; Wroe et al., 2008).

The utility of bite force estimation as a tool extends across multiple fields, including paleontology, because this metric may provide insights into evolutionary modifica-

tions, feeding strategies, and diets (Sakamoto, 2022; Wroe et al., 2008). This method of estimating organismal performance has been validated live in multiple taxa, including crocodiles (Erickson et al., 2012; Erickson et al., 2014; Sellers et al., 2017), turtles (Herrel and O'Reilly, 2006; Marshall et al., 2012; Pfaller et al., 2011;), fish (Grobeck and Pietsch, 1979; Grubich et al., 2008; Grubich et al., 2020) and elasmobranchs (Habegger et al., 2012; Huber and Motta, 2004; Mara et al., 2010). While monkfish are amenable to captivity and can be studied live, practical challenges, such as maintaining them in a controlled environment, make the acquisition of deceased specimens an alternative for bite force analyses.

In biology, a trade-off refers to the compromises between different traits or functions in response to ecological pressures (Abbink et al., 1999; Charpentier, 2015). Bite force estimates are derived from the combined action of the jaw closing muscles and the biomechanics of the lever system of the mandible (Huber and Motta, 2004). A trade-off for lever-based systems is the prioritization between force and speed, meaning that a single lever system cannot be strong and fast at the same time (Abbink et al., 1999). Typically, long jaws are specialized for speed, while short jaws are used for a forceful bite (Morales-García et al., 2021). This is because as the length of the jaw increases, the relative height of the articular decreases (Figure 1). This growth changes mechanical advantage, which is a measure of how effectively a lever system amplifies speed or force. Longer jaws bring the ratio of mechanical advantage towards a value of 0, while shorter jaws shift it towards a value of 1.

This study aims to 1) quantify bite force in the American monkfish using bite force estimation, and examine how this scales with size, and 2) identify the primary contributor to bite force generation, either quadratomandibularis (QM) mass (the primary jaw closing muscle) or mechanical advantage. While the amount of force generated is dependent upon the strength of the muscle, mechanical advantage is a measure of

how effectively a lever system amplifies force or speed. We also hypothesized that monkfish would trend towards force optimization rather than speed optimization in terms of the jaw closing system, due to their relatively short jaws, and what is known about diet (see next section).

Biology of Monkfish

The American monkfish (*Lophius americanus*) belongs to the family Lophiidae, within the order of Lophiiformes. Lophiiformes, also known as anglerfish, are a group of bony fishes characterized by their unique appearance (Steimle et al., 1999). These fishes are known for their modified dorsal fin rays that are a lure (illicium) with bait (esca) at the tip that is used to attract prey (Erasmus et al., 2018; Gordo and Macpherson, 1990). Anglerfishes live in the deep-sea and have modifications to these extreme environments, including bioluminescence (Bassot, 2015). Lophiiformes encompass 322 different species that have varying body shapes and sizes, ranging from 20 cm - 1.5 m (Miya et al., 2010). Within the family Lophiidae, American monkfish are most closely related to European monkfish (*Lophius piscatorius*) and the anglerfish (*Lophius litulon*). They share many morphological and ecological characteristics (Steimle et al., 1999).

Monkfish are bottom dwellers who spend most of their lives on the ocean floor, tolerating a wide range of temperatures and depths up to 750 m (Richards et al., 2010). American monkfish are found partially covered with sand or mud on the seafloor and drift with the bottom currents to assist in migration. American monkfish live along the continental shelf in the western North Atlantic but have been found in the Gulf of Mexico and the coast of Barbados (Baird, 1871). Although they primarily dwell at the bottom of the ocean, they swim towards the surface of the water during breeding season and to hunt birds (*Monkfish And Gulls*, 1933). Natural predators of

monkfish, therefore, are few, but include sharks, thorny skates, and swordfish (Gordoa and Macpherson, 1990).

Monkfish are characterized by a broad head, large mouth, and flat, tapered body; they lack scales and appear smooth and slippery. It has eyes described as “dark and beady” that sit on top of the head (Caruso, 1989). Monkfish fins have fleshy textures. The carpal bones (wrist bones that connect to metacarpal bones) are elongated with fin webbing between them, allowing the fins to unusually bend (Richards et al., 2010). The pectoral fins of anglerfish are found in front of the gills rather than behind, and pelvic fins are placed anteriorly under the head rather than the chest (Angus, 2003). Monkfish are pediculate fish, meaning that the pectoral and ventral fins are sturdy enough that the fish has been documented “walking” on the seafloor (Richards et al., 2010).

Monkfish are a carnivorous species that have flexible, rubber-like skin allowing the stomach to stretch to accommodate meals (Gordoa and Macpherson, 1990). Monkfish have unusually wide ribs, which allows food to slip past the rib cage and into the stomach. With their large mouth and stomach, monkfish can engulf prey of nearly their own size. Monkfish have a modified dorsal fin that is used as a lure, to draw a prey item closer to the mouth. Once the prey is close enough, the buried monkfish uses suction to engulf the prey (Valentim et al., 2008). The American monkfish possesses dark brown skin on the dorsal side and pale white skin underneath, making them easily distinguishable from other monkfish species (Johnson et al., 2008); a coloration also presumably useful for remaining cryptic when on the substrate. This feeding strategy, combined with their sharp teeth, allows the monkfish the element of surprise, and presumably affords a certain amount of foraging efficiency, with minimal energy expenditure invested in stalking or hunting the prey item (Solmundsson et al., 2010).

The dietary preferences of monkfish exhibit a notable transition throughout their life stages. During the larval stage, monkfish predominantly feed on zooplankton. As they progress into juveniles, their diet expands to include small fish, shrimp, squid, and sand eels. Adult monkfish have a more diverse array of prey, making a shift towards larger and more varied items, as well as a mix of both elusive and defended prey. They prey on large fish, crabs, lobsters, octopuses, squid, mollusks, seabirds, diving ducks, other monkfish, and even sea otters. This pattern suggests a correlation between monkfish size and the size of their prey, indicating a dynamic relationship in their feeding ecology (Armstrong and Colvocoresses, 1992; Johnson et al., 2008).

A distinctive feature of the American monkfish is their fang-like teeth (Baird, 1871). The sharp needle teeth, varying in size, form rows along the oral, or anterior, jaws and curve backward toward the esophagus. Additionally, they sport hundreds of smaller pharyngeal teeth that line the roof of the mouth posteriorly, and frame the opening to the esophagus. Monkfish use suction to engulf their prey, and then trap it using these specialized teeth. The teeth are putatively designed for immobilizing prey by gripping it, and moving it in a sawing motion between the oral and pharyngeal jaws, moving the food towards the esophagus, rather than tearing or chewing. (Gordoa and Macpherson, 1990; Wilson, 1937). Varying from a typical “bite,” this raises questions about the mechanics of their bite and potential trade-offs in terms of force production.

Anglerfish, in general, are also known for their reproductive behaviors, specifically when males fuse themselves to females and become permanent parasites (Isakov, 2022). However, this particular feature is not found in monkfish. The mating season for American monkfish occurs between February and October, when both males and females release their reproductive cells into water, allowing females to produce up to 1 million eggs per season (Johnson et al., 2008). The eggs are laid in a single layered ‘veil’ that floats at the ocean’s surface. The mucous sheet of eggs is 6 - 12 m long and

up to 1.5 meters wide. Depending on the temperature, larvae hatch from the eggs within 5 - 100 days. They are pelagic and join the ichthyoplankton community until they reach 3 inches in length and are ready to descend into deeper waters. Growth is fast in the first year, but slows over time (Armstrong and Colvocoresses, 1992). American monkfish can reach total lengths of 40 cm - 1.5 m, with females typically surpassing males. The American monkfish has a lifespan of up to 13 years, reaching sexual maturity at 3-4 years, and weighing around 23 kg at this age (Armstrong and Colvocoresses, 1992).

Materials and Methods

American monkfish, *Lophius americanus*, were collected from the North Atlantic during a survey cruise conducted by the National Oceanic and Atmospheric Administration (Figure 2). The specimens were frozen for transport, shipped, and then placed in freezers until morphological analyses were initiated in the laboratory at Arizona State University. A total of 27 specimens were suitable for analysis (17-51 cm total length; TL). There was a limited availability of total weight data (19 specimens, 98 - 4754 g) due to these measurements not recorded at the time of the study. Total weight may not have been considered critical or relevant to the initial research question. These specimens were thawed, skinned, and dissected to expose the quadratomandibularis muscle (Huber and Motta, 2004). Images of the exposed muscle were taken using Nikon Coolpix P530 and D3500. Muscles were excised, weighed, and stored in 70% ethanol.

The pictures of the exposed muscle were imported into NIH ImageJ Version 1.53j 13 (Rasband, 1997), which was used to make measurements required to calculate the physiological cross-sectional area (PCSA), mechanical advantage, theoretical maximum tetanic tension, and force production. We note here that the quadratomandibu-

laris, the primary jaw closing muscle, had no apparent divisions and was treated as one muscle. The PSCA is the cross section of perpendicular muscle fibers and is used to show the contraction strength of the muscle (Martin et al., 2020). Physiological cross-sectional area was calculated according to the Powell et al. (1984):

$$PCSA = \frac{\text{quadratomandibularis mass} \cdot \cos \Theta}{FL \cdot \text{muscle density}}$$

where Θ refers to the average angle of pennation, FL refers to average the muscle fiber length, and the density of fish muscle is 1.05 g/cm^3 . Average angle and fiber length values were calculated using ten separate measurements taken from a picture of the quadratomandibularis muscle. Angle measurements were taken by finding the angle between a line drawn along a distinct muscle fiber and a line drawn along the muscle line of action, while fiber length measurements were taken by drawing a line from end to end of a distinct muscle fiber. Mechanical advantage for the muscle was calculated by dividing the muscle in-lever length by the lower jaw out-lever length (Figure 3). In-lever lengths were measured by drawing a line from the point of jaw articulation to the region of the muscle attachment in close proximity to the muscle center of mass and central tendon. The out-lever length was determined by measuring the line from the point of jaw articulation to the anterior-most tooth of the lower jaw. Theoretical maximum tetanic tension (P_o) was calculated according to the formula (Powell, 1984):

$$P_o = PCSA \cdot \text{specific tension}$$

where PCSA refers to the calculated physiological cross-sectional area, and the specific tension used was that of vertebrate muscle, which is 20 N/cm^2 . Theoretical maximum tetanic tension was used to calculate the maximum force a muscle can generate when fully contracted. Calculated P_o values were doubled to account for the muscles of both sides of the body. To isolate the component of muscle force which acts in line

with the muscle direction of action, the perpendicular component of P_o , $\perp P_o$, was determined trigonometrically with the formula (Huber and Motta, 2004):

$$\perp P_o = \sin \theta \cdot P_o$$

where θ refers to the angle between the muscle in-lever and the muscle line of action. According to the formula (Wainwright and Richard, 1995; Cutwa and Turingan, 2000):

$$\text{ForceOut} = \perp P_o \cdot \frac{LI}{LO}$$

the theoretical maximum force produced by the muscle (the output force associated with the muscle out-lever) was calculated by multiplying $\perp P_o$ (the input force associated with the muscle in-lever) by the muscle's mechanical advantage ratio.

In order to investigate how bite force scales with size, the relationship between bite force vs. total length (TL) and bite force vs. body mass were analyzed using linear regression. Both total length and body mass were used as indicators of size as many studies often use one or the other. We present both to aid in comparing these results to other species. Each regression against a size variable, total length or body mass, was performed separately.

The relationships between QM mass vs. size and mechanical advantage vs. size were also explored, to better understand what might be driving the relationship between bite force and size. In these analyses, we used only body mass as the size variable, and did not further explore relationships with total length, as the predicted scaling relationships with mass are much more straight-forward. Mass has biological relevance, with many physiological and metabolic functions being closely related to body mass (Gillooly et al., 2001; Nagy, 2005). Total length, however, can be more variable and is not typically indicative of muscle growth (Hilborn and Walters, 2013).

Slope, R^2 , and p-values were found using Microsoft Excel and StatTrek T Dis-

tribution Calculator. TT-tests comparing the slope of the line to a slope of 0, as is standard for linear regression, were performed on all regressions.

Diet data was also obtained through dissections of all stomachs and intestines, followed by the excision and careful examination of their contents. Prey items were identified to the lowest possible taxonomic level. While this is not meant as a comprehensive study of monkfish diet, this represented an opportunity to validate literature descriptions of the diet.

Results

The regression of bite force against total length had a slope of 1.16. The model was not a good fit to the data ($R^2 = 0.255$). The slope was significantly different from a slope of zero ($P \leq 0.001$), but the poor fit of the line to the data makes any inference about this slope weak at best. Because the line was such a poor fit to the data, we did not examine any additional comparisons of this slope to other hypothetical slopes, like a slope of 1. (Figure 4A).

The regression of bite force against mass had a slope of 0.0134. The model was a strong fit to the data ($R^2 = 0.916$), and, despite being rather close to zero, the slope was also significantly different than a slope of zero ($P \leq 0.001$) (Figure 4B).

The regression of QM mass against body mass had a slope of 0.00791. The model was also a strong fit to the data, and the slope statistically significantly different compared with a slope of zero ($R^2 = 0.973$, $P \leq 0.001$) (Figure 5).

The slope for the regression of mechanical advantage against body mass was -1.97×10^{-7} ($R^2 \leq 0.001$, $P \leq 0.001$). The model was not a good fit to the data, and the slope was not statistically significant from a slope of zero ($P = 0.059$) (Figure 6).

Table 1: Stomach contents of American monkfish presented with total lengths.

Specimen Total Length (cm)	Items found
25.857 cm	Small starfish; 4 squid; 1 eel, 1 unidentified fish, 1 small pompano
28.373 cm	1 eel
36.706 cm	1 eel
42.467 cm	Possible shells
42.981 cm	2 squid

Discussion

Considering their feeding strategy, and observations of closely related species in captivity, we hypothesized that monkfish would trend towards force optimization rather than speed optimization in terms of jaw closing, or bite force (Grubich et al., 2020; Mara et al., 2010). However, the main finding of this study revealed that while bite force does increase with size, it is only a slight increase. In particular, the relationship between bite force and body mass, while a non-zero relationship, seemed low. The very slightly positive slope for bite force versus body mass would seem to imply that increases in bite force are not even keeping up with simple body growth. If bite force scaled with body growth, expressed as mass, we would expect the slope to be closer to 1. It was also observed that mechanical advantage remained more or less constant across the sizes of individuals sampled. As mechanical advantage is a dimensionless ratio, this result might be reasonably expected. This means, practically-speaking, that regardless of size, the jaws perform at the roughly the same efficiency.

The findings support a generalist biting strategy rather than specialization to-

wards extreme force (or extreme speed). Considering what is known regarding their prey capture methods, and that the primary capture method involves trapping and engulfing prey (Valentim et al., 2008), the necessity for a strong bite may be relatively diminished. Conversely, if suction is a predominant mechanism for drawing prey fully into the mouth, which is an act associated with jaw opening, then extreme speed from the jaw-closing system may not be necessary. Thus, it may be the case that neither extreme force nor extreme speed is needed to facilitate prey capture in monkfish.

However, bite force may be assisted, in a sense, by the teeth. Monkfish have a distinctive dental morphology, as noted previously, characterized by smooth and slender teeth. Unlike serrated teeth, which are ideal for cutting or tearing, smooth teeth are better suited for puncturing and piercing (Whitenack and Motta, 2010). The smooth surface allows for the concentration of a significant force on the tooth's edge, generating high pressure that aids in puncturing materials. This is particularly advantageous for consuming prey such as crabs or mollusks. This means that even without a notably strong bite force, monkfish can focus the force that is generated at the tooth points, increasing its effectiveness on hard prey (Whitenack and Motta, 2010).

If we compare the results discovered here, for American monkfish, with other published bite force data, we find that small monkfish produce a bite on par with other, similarly-sized species. The data for some of the smallest monkfish in this study are included in Table 2. The bite force for these specimens was comparable to smaller yellowhead wrasses (*Halichoeres garnoti*), which are carnivores that eat mainly mollusks and crustaceans (Deady and Fives, 1995). However, larger monkfish show bite forces that seem to exceed similarly-sized fishes, at least given the available published data. Table 2 also includes both the average, and some of the very largest monkfish in this study. The largest monkfish are capable of producing a bite much stronger than large

wahoo or mackerel, at least as predicted by the estimation methods used here. Wahoo are generalist feeders, consuming pelagic fishes, and the individual compared in this study was approximately three times heavier than our largest monkfish (Franks et al., 2007). The diet of mackerel consists of shrimp and krill (Kock et al., 1994). We also included in Table 2 bull sharks (*Carcharhinus leucas*) and white sharks (*Carcharodon carcharias*). These species are very obviously much stronger biters than monkfish, but were included to give a sense of the extremes, at the upper end of the spectrum in terms of bite force.

These totality of the findings presented here collectively underscore the complexity of predatory capabilities of monkfish and highlight the need for further exploration and understanding of their unique feeding behaviors. Future studies might focus on live measurements of force, exploring additional studies on wild feeding behaviors to understand their dietary preferences and capture techniques, and feeding kinematic studies to gain a comprehensive understanding of the functional mechanics of their jaws. Despite these future directions that might still be needed to more fully understand how American monkfish capture prey with their unique morphology, there are several ways in which the present findings can be leveraged.

This study of bite force monkfish can contribute to aspects of ecosystem conservation and management. Monkfish, as multi-level predators in marine ecosystems, play a crucial role in regulating populations throughout various levels of the food chain during their lifecycle. Understanding the mechanisms by which monkfish capture their diverse prey contributes valuable insights into their potential to impact these food chains. For example, knowing now how important the bite is, or is not, and how this aids in prey capture, one might reasonably assume that this species is unlikely to have significant impacts on populations of fast moving and large prey, like diving birds or sea otters, but may have notable impacts on medium-sized fish and

shellfish communities. The latter two sorts of food items may be common foods for other predators in the ecosystem. Thus, this research aids in better managing ecosystems, and conservation efforts can be more effectively tailored to sustain monkfish populations as well as maintain the balance of lower-level predators and prey species.

This study may also be of value from the perspective of commercial fishery management. Given their abundance, they are considered to be ‘above target population levels.’ Thus, monkfish stand out as an environmentally conscious seafood choice (Monkfish, 2023). Monkfish are commonly caught in trawls by fleets extending from Maine to North Carolina (Monkfish, 2023), with nearly all monkfish sales in the US originating from domestic fisheries. The 2022 commercial monkfish yield reached 14 million pounds, and was valued at \$13 million. Known for having a taste similar to lobster, monkfish has earned the nickname of the “poor man’s lobster.” Its culinary appeal has contributed to its popularity in standalone dishes and as a component in traditional lobster-based recipes. Given this appeal, it seems likely that commercial fishing efforts for American monkfish will increase. Thus, the findings of this study provide practical knowledge for sustainable fisheries management, again considering their role in a larger ecosystem, including how they interact with other potentially important commercially-fished species (ie., molluscs, other fish).

Finally, this study may prove valuable for the emerging practice of monkfish aquaculture, in that we know more about how monkfish eat and what can be fed to monkfish in captivity to ensure their diverse diet needs are met (Ragasa et al., 2022; Kaleem and Bio Singou Sabi, 2020). It is noteworthy that some fish-farming practices resort to feeding the equivalent of ‘fish chow’ in order to facilitate rapid growth and marketability. This commercial chow actually leads to the production of fish that are unhealthy for humans to consume, as they have the wrong composition of omega fatty acids (Alam et al., 2014). With the present study, a more practical, and natural,

dietary source could be derived by aquaculturists.

Table 2: Comparison of American monkfish bite force estimates with published data from other fish species.

Species Name	Mass (kg)	Average Bite Force (N)
Yellowhead wrasse ¹ (<i>Halichoeres garnoti</i>)	0.021	10
Black belly lanternshark ² (<i>Etmopterus lucifer</i>)	0.048	3.1
Small American monkfish (<i>Lophius americanus</i>)	0.098	11.23
Piranha ³ (<i>Pygocentrus nattereri</i>)	0.63	49.51
Spotted ratfish ⁴ (<i>Hydrolagus colliei</i>)	0.87	106
Spiny dogfish ⁵ (<i>Squalus acanthias</i>)	1.065	19.6
Average American monkfish (this study) (<i>Lophius americanus</i>)	1.49	37.23
Bonnethead shark ⁶ (<i>Sphyrna tiburo</i>)	2.24	25.7
Large American monkfish (<i>Lophius americanus</i>)	4.75	87.72
Kingfish mackere ⁷ (<i>Scomberomorus cavalla</i>)	5.7	19.3
Wahoo ⁸ (<i>Acanthocybium solandri</i>)	18.2	29.2

Continued on next page

Table 2: Comparison of American monkfish bite force estimates with published data from other fish species. (Continued)

Species Name	Mass (kg)	Average Bite Force (N)
Bull shark ⁹ (<i>Carcharhinus leucas</i>)	140.34	1023
White shark ¹⁰ (<i>Carcharodon carcharias</i>)	1329	8641.3

¹ Clifton and Motta (1998); ² Huber (2006); ³ Grubich et al. (2020); ⁴ Huber et al. (2008);
⁵ Huber and Motta (2004); ⁶ Mara et al. (2010); ⁷ Ferguson et al. (2015); ⁸ Habegger et al.
(2017); ⁹ Habegger et al. (2012); ¹⁰ Wroe et al. (2008)

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APPENDIX

FIGURES

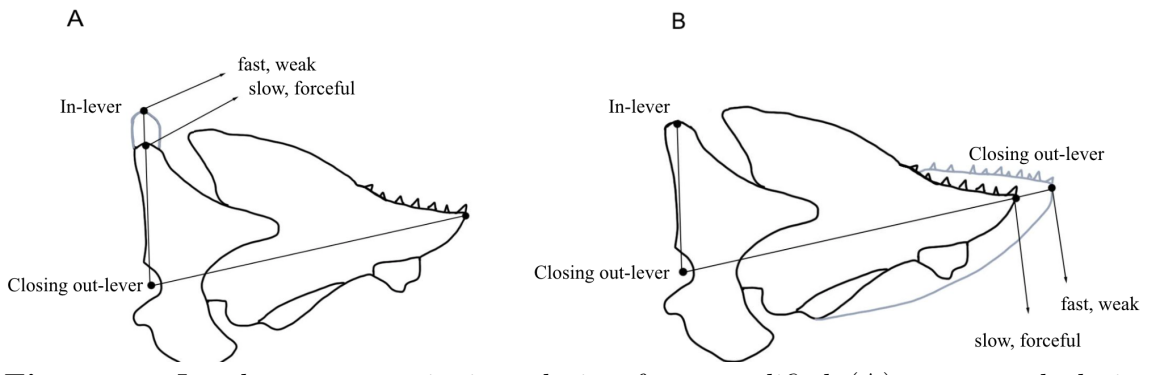


Figure 1: Jaw lever system in jaw closing force modified (A) vs. speed closing modified (B)

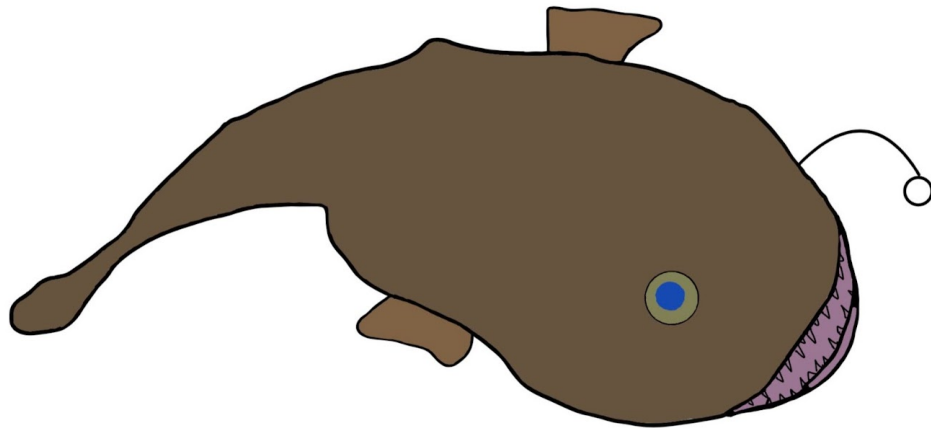


Figure 2: American monkfish (*Lophius americanus*) drawn from thawed specimens. Drawing by the author.

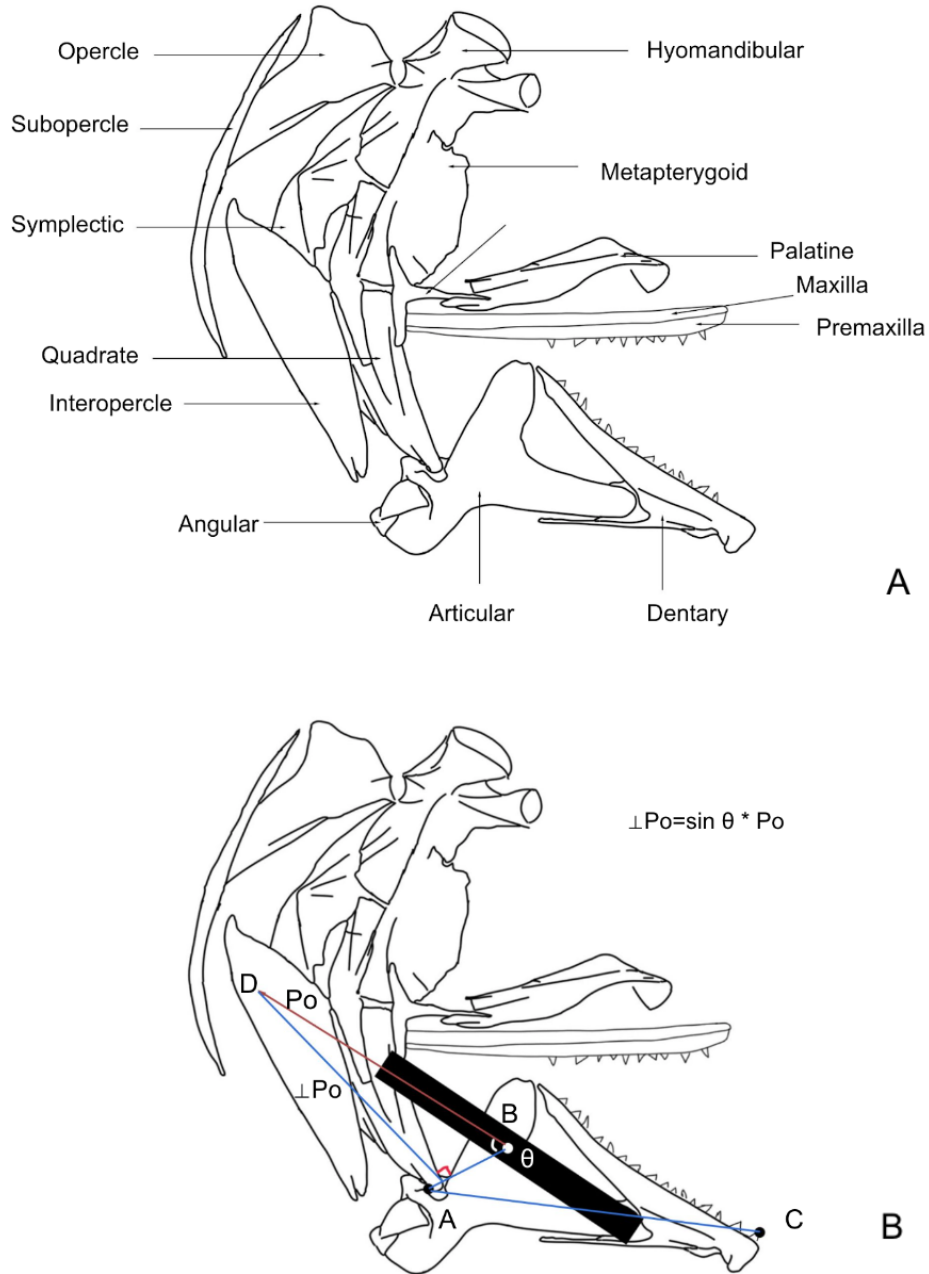


Figure 3: Select cranial and jaw bones in monkfish skeleton (A), and jaw-closing levers and force vectors (B). Line AB, in-lever; AC, out-lever; BD, muscle force vector; P_o , maximum tetanic tension; $\perp P_o$, component of P_o perpendicular to the in-lever; θ , angle between the in-lever and muscle force vector. Drawing by the author.

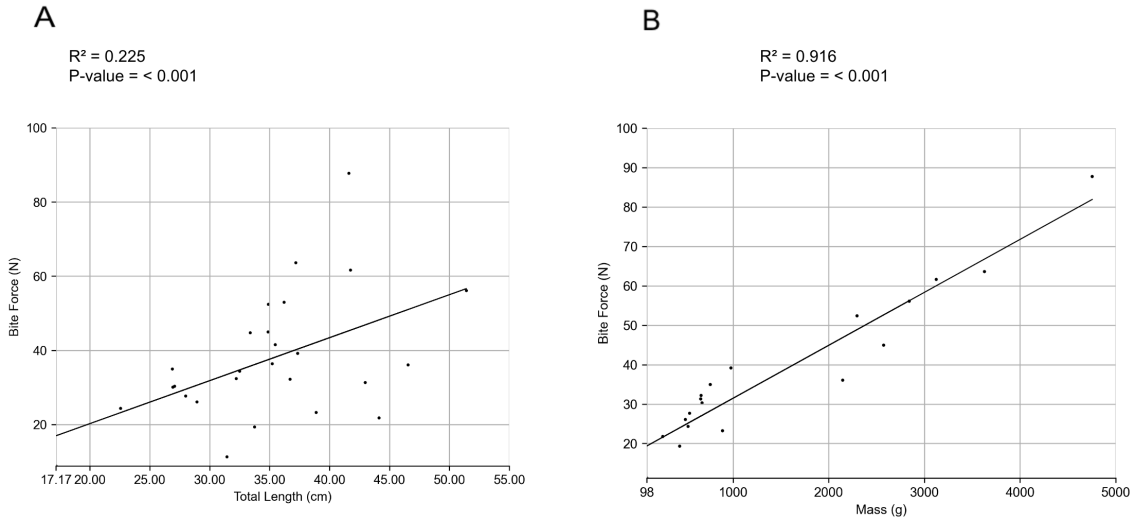


Figure 4: Regressions of bite force against size; total length (A), and mass (B). Black line depicts linear regression. Green line depicts the null hypothesis, or 1:1 slope. Shown are R^2 and p-values for each regression.

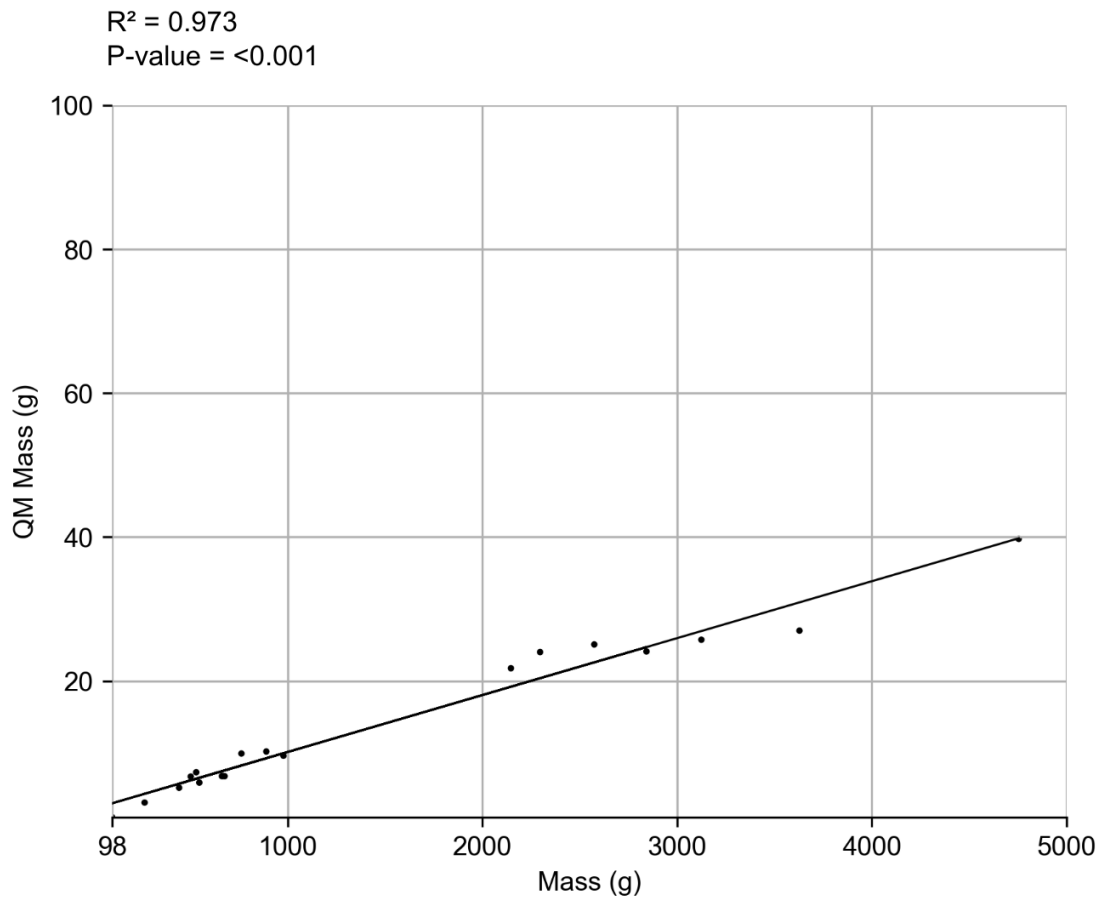


Figure 5: Regression of QM mass against body mass. Green line depicts the null hypothesis, or 1:1 slope. Shown are R^2 and p-values.

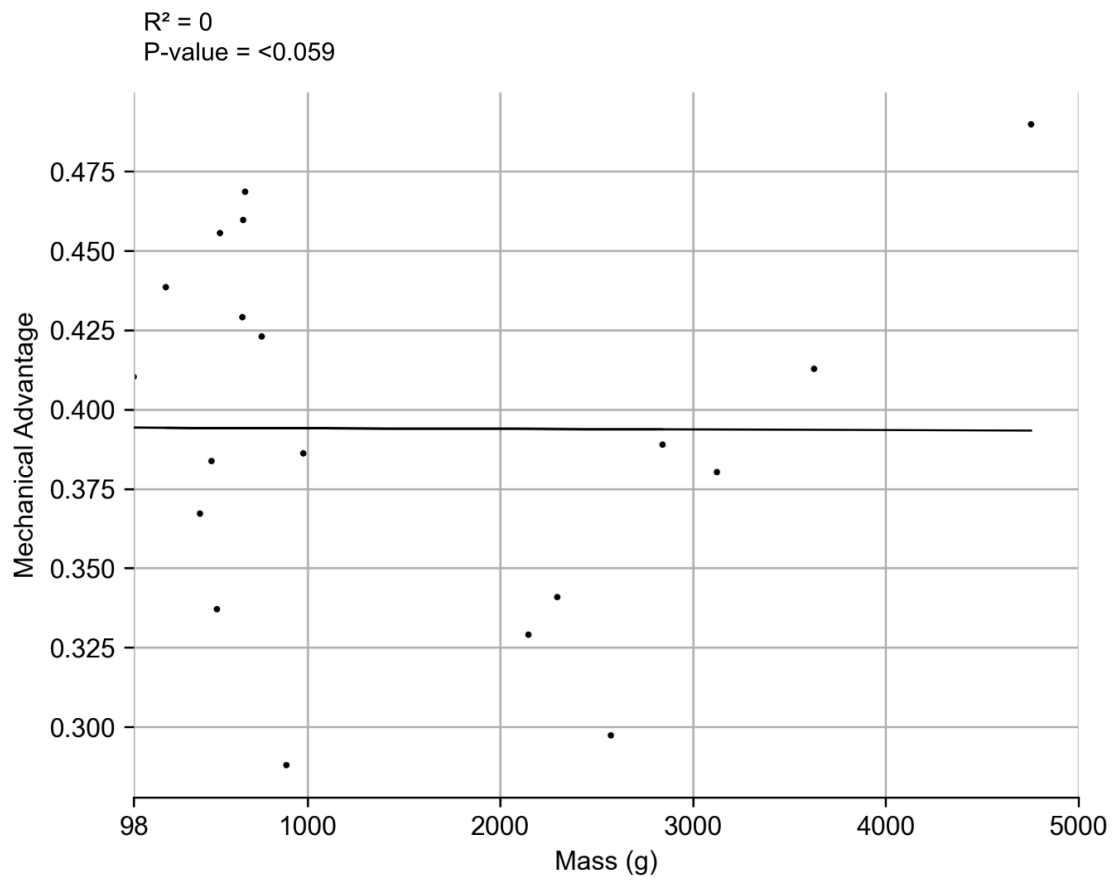


Figure 6: Regression of mechanical advantage against mass. Slope is drawn even though the relationship is not significant. Shown are R^2 and p-values.