

Why the Round Head? Morphometrics relating to Ontogeny of Select Bulbous Fishes

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ABSTRACT

Potential effects of changing body shape morphometrics with growth in bulbous fishes were studied in five species; *Clinocottus globiceps*, *Oligocottus maculosus*, *Liparis dennyi* and *Gobiesox maeandricus* and *Chitonotus pugetensis*, all found and collected in the Salish Sea, Washington. For each species there was a size range that attempted to encompass juvenile to adult forms. We evaluated the standard length, body width and body depth along the length of the body of each individual. To understand how body streamlining and structural stiffness change with growth we calculated second moment of area and aspect ratio. We found a significant correlation between ontogeny and change in body shape and stiffness. As these fish grow in length they become more streamlined along the body and increase stiffness of their wide heads. Changing body morphometrics with growth have important implications about fish's swimming performance, predator avoidance, obtaining food and maneuvering within their habitat.

INTRODUCTION

Morphometrics refers to the quantitative analysis of body form. Fish morphometrics are commonly performed in studies and are helpful in analyzing developmental changes in body shape. It is used to deduce changes relating to ontogeny, function and phylogenetic relationships. Traditional morphometrics examines sizes such as lengths, widths, depth and ratios (Marcus, 1990). In this study we will use body morphometrics to statically test our hypothesis about how body shape and structural stiffness change with growth in tadpole shaped species.

When looking within the same species with varying lengths an understanding of ontogeny can be achieved. Using a range of small juveniles to large adults we can measure the rate of growth and find differences of maximum structural stiffness and aspect ratio. We can also see how these measurements change along the body. As some fish age they grow to be wider than deep, like flat fish whereas others become deeper than wide, like the bluefin tuna. Swimming mechanics, habitat and prey and predator interactions are all dynamic variables that change as fish age; these variables contribute to why and how body form changes with growth. Having a clear understanding a species ontogenetic development tells researchers about potential characteristics that are beneficial to the fish's needs during that phase of their life (McHenry and Lauder, 2006).

Aspect ratio and relative body stiffness are good predictors for fishes swimming performance. A more streamlined and stiffer fish would be able to escape predators, capture prey efficiently and have less drag when they swim. A fish with a low drag body shape has the ability to swim at various speeds without heavily increasing the energy cost of locomotion (Pettersson and Hedenstrom, 2000). A less streamlined and less stiff fish would have greater challenges swimming efficiently and would have a greater surface area exposed, creating a larger overall drag. Fish with a high drag body shape experience large increases in energetic costs from small increases in swimming speed. Stiffness is measured using engineering structural beam theory where the cross section of a fish is assumed to be an ellipse which major and minor axes are then put into an equation to calculate. The second moment of area (in units of m^4), yields a flexural stiffness of the beam (Porter et al., 2009). The body shape can be quantified as an aspect ratio of the body, which is a measurement giving insight to the streamlining of the fish. Both of

these measurements are good predictors into locomotive mechanics of fish.

We studied five species with bulbous shaped heads and elongate bodies belonging to three families. These fishes are predominately benthic, live in intertidal zones and tend to be weak swimmers. Typical prey includes crustaceans and small fish. Within the Scorpaeniformes we examined species in the Cottidae and Liparidae families. Species studied within these families have interesting similar tadpole-like bodies. Similar characteristics include large bulbous heads with small eyes and tapering slender bodies to a very small tail (Smith and Wheeler, 2004). We also examined *Gobiesox maeandricus*, which is not in the order Scorpaeniformes but has a very similar tadpole body shape. The fish selected to examine body morphometrics were chosen due to their similar body shapes and similar habitat of the Salish Sea.

In order to investigate morphological growth changes we related body measurements to second moment of area and aspect ratio in bulbous shaped fishes. Our research focused on three specific questions: (1) how does structural stiffness change along the body? (2) how does body shape and stiffness change with growth? (3) how do similarly shaped bulbous fishes compare when looking at body shape and stiffness? We predicted that stiffness would decrease along the body since the species studied all have characteristically wide heads and slender bodies. We also hypothesized that maximum aspect ratio and stiffness would increase with ontogeny and be similar when looking at different tadpole shaped species.

MATERIALS AND METHODS

Specimens and anatomical measurements

We examined five species of tadpole shaped fishes; the marbled snailfish (*Liparis dennyi*: Liparidae), the northern clingfish (*Gobiesox maeandricus*: Gobiesocidae), the mosshead sculpin (*Clinocottus globiceps*: Cottidae), the tidepool sculpin (*Oligocottus maculosus*: Cottidae) and the roughback sculpin (*Chitonotus pugetensis*: Cottidae). Each species had a range of size doubling in standard length or more. All specimens were obtained from Friday Harbor Labs fish collection. Collections were made from 1950-2012 within the Salish Sea using various methods including otter trolls and beach seining. All individuals were preserved in 70% ethanol and kept in glass collection jars.

Body dimensions were measured from the marbled snailfish (*L. dennyi*, N = 10), the Northern clingfish (*G. maeandricus*, N = 15), the mosshead sculpin (*C. globiceps*, N = 14), the tidepool sculpin (*O. maculosus*, N = 4) and the roughback sculpin (*C. pugetensis*, N = 17). For each specimen, total body length (snout to tail tip), maximum body depth and maximum body width were taken as preliminary measurements. We used a digital Cannon T2i on a standard vertical copy stand (Fig. 2) to photograph every individual. Specimens were handled minimally and placed onto a grey velvet material with a ruler and then were photographed from the dorsal and lateral view. We then quantified photographs on the image-processing program, ImageJ. Standard length (SL) was measured from snout to caudal peduncle (Fig. 3A). Body width (BW) was measured using the dorsal view and ran parallel to the specimens eyes. Body depth (BD) was measured using the lateral view and was from dorsal to the ventral, excluding all fins. Both BW and BD were measured at ten percent intervals of the SL along the body (Fig. 3A and 3B).

Statistical analysis

All data was tested in JMP 10. In order to quantify how streamlined a body is we calculated the aspect ratio (AR) maximum BW divided by maximum BD. Using a linear regression we graphed AR_{MAX} against standard length per species (Fig. 4). We plotted AR along the standard length percent to acquire a slope from maximum AR to lower average AR. This slope was standard within one species but varied between species and was usually from twenty percent to sixty percent of the SL of the specimen. We took the mean of the slope of each species, AR_{MEAN} , and then performed an ANOVA to calculate variance and to find statistical significance between the species tested (Fig. 7B). Aspect ratio is normalized to the specific sample and therefore can directly compared between species. Standard errors were calculated and are shown on the bar graph.

In order to test for structural stiffness of individuals we calculated second moment of area. In our calculations we assumed that the transverse shape of the fish we measured were elliptical. The second moment of area, I (m^4) for all individuals was calculated with the following equation:

$$I = \pi/4 * [(BD/2)/100] * [(BW/2)/100]^3$$

where BD is body depth (cm) and BW is body width (cm). They were divided by two, which transformed the measurements from diameter to radius of the ellipse and divided by one hundred to change units from centimeters to meters. Measurements of BD and BW were used to calculate the maximum second moment of area, I_{MAX} , and the second moment of area of ten percent intervals along the standard length of the body.

We graphed I along the length of the body for each individual (Fig. 6). The slope from I_{MAX} to average low I varied between species but was constant within one species

and was tended to be from twenty percent to fifty percent of the standard length. All slopes were negative because of the decrease of I along the body. The mean of the slopes per species, I_{MEAN} , was then run through an ANOVA to compare significance between species (Fig. 7A). Standard errors were calculated and shown on the bar graph. We ran a linear regression of I_{MAX} and standard length per species (Fig. 5).

A significance level of $P \leq 0.05$ was used to determine significance of statistical tests performed.

RESULTS

MAXIMUM ASPECT RATIO

As determined by linear regression of our data *L. dennyi*, *G. maeandricus*, and *C. pugetensis* showed positive correlation of maximum aspect ratio and increasing standard length when measured from both the photographic lateral and dorsal views. While aspect ratio did increase with increasing standard length, the ratio increased by less than two times (Fig. 4). *G. maeandricus* showed the most rapid increase in aspect ratio with increasing standard length (slope = 0.1, $R^2 = 0.524$; $P = 0.002$). In these three species the widest region of the fish becomes wider as they grow in length. *O. maculosus* and *C. globiceps* showed no statistical significance of aspect ratio with respect to ontogeny. The aspect ratio of all individuals of all species tested ranged from 1.06 to 2.58, meaning that all species maximum width section was wider than deep.

SLOPE OF MAXIMUM ASPECT RATIO

When comparing slope of maximum aspect ratio, AR_{SLOPE} , across species, *L. dennyi* and *G. maeandricus* were significantly different as determined by ANOVA

($F_{4,52}=16.90$). The other species were statistically indistinguishable from one another. The slope at which the aspect ratio decreases along the length of the body varies between species (Fig. 7A). Student's t-test showed that *G. maeandricus* had the greatest AR_{SLOPE} of -2.65 whereas *O. maculosus* had the lowest AR_{SLOPE} of -0.868.

MAXIMUM SECOND MOMENT OF AREA

There was a highly similar trend with the five species of second moment of area along the body. From juvenile to adult the average fish had the greatest second moment of area at around twenty percent of the standard body length, which was the head area of the fish. The stiffness then had a steep decline in from thirty percent to sixty percent, the area transitioning from the head to the body, and then tapered off to nearly zero nearing the caudal peduncle (Fig. 6). In each species the standard length was a factor in how second moment of area changed along the body. With a large standard length I_{MAX} was noticeably larger and the first decline slope was much more steep, whereas the smaller standard length fish had a much less noticeable increase of I_{MAX} and a less steep slope. The body shape of *C. pugetensis* differs from the other, being thinner with no bulbous head. However, these general trends were similar in all five species tested.

As shown by linear regression, maximum second moment of area, I , differed among species and increased significantly in as SL increased (Fig. 5). This trend was continuous in all species and was reflected in our measurements. *G. maeandricus* showed the most rapid increase of maximum second moment of area as SL increased. *G. maeandricus* ($R^2 = 0.861$; $P < 0.001$), and *C. pugetensis* ($R^2 = 0.847$; $P < 0.001$) both had the largest I_{MAX} which was nearly six times the value the I_{MAX} of *L. dennyi*. As an overall trend all species showed increased stiffness with ontogeny.

SLOPE OF MAXIMUM SECOND MOMENT OF AREA

When comparing the slope of second moment of area, I_{SLOPE} , across species, *C. pugetensis* and *G. maeandricus* were significantly different as determined by ANOVA ($F_{4,52}=2.52$). The other species were statistically indistinguishable. The slope at which the aspect ratio decreases along the length of the body varies between species (Fig. 7B). Student's t-test showed that *G. maeandricus* had the greatest I_{SLOPE} of $-4.6185e^{-8}\text{m}$ whereas *O. maculosus* had the lowest I_{SLOPE} of $-2.96e^{-9}\text{m}$.

DISCUSSION

How does body shape change during growth?

Maximum aspect ratio was found on average at twenty percent of the standard length, which was the widest section of the organisms' head. We found a significant correlation of increasing maximum aspect ratio with increasing standard length in *L. dennyi*, *G. maeandricus* and *C. pugetensis* (Fig. 4). This shows that as these species grow in length their head increases in width. Overall the general body shape becomes more streamlined, excluding their head sections. This correlates with our hypothesis that maximum aspect ratio increases with increasing lengths. These findings agree with previous studies where body streamlining increases during growth in fish (McHenry and Lauder, 2006). Before we collected our data we hypothesized that these select species would have a fairly constant low aspect ratio, meaning a rounded body, from juvenile through adult stages; however we found this not to be true. Even in *O. maculosus* and *C. globiceps*, where the statistics were not significant, there were noticeable increases in maximum aspect ratio with increasing lengths. It is possible that *O. maculosus* and *C.*

globiceps had too small of sample sizes, or because the size range tested was too small within the species. If there were not a large enough sample size range then measuring a change in body shape with respect to growth would be harder to find significant results. This could explain why *O. maculosus* and *C. globiceps* were statistically insignificant when looking at maximum aspect ratio with respect to growth. *G. maeandricus* had the largest rate of maximum aspect ratio increase out of the species measured, showing that as *G. maeandricus* grow their heads become significantly wider than deep.

Body shape is a diverse and complex morphology that integrates a whole array of mechanisms including genetics, internal systems, whole systems and ecology. Since body shape affects whole body properties it heavily influences performance and ability of an array of behaviors (Walker, 2010). Body shape is a multivariable inquiry, however by looking at specific morphometric measurements and calculations we can have a greater insight into ontogeny. Body depth and width may be dependent on complex interactions of predation and habitat. Shallower body depth correlates to a decreased hydrodynamic drag that has associated energetic gains that would be beneficial in escaping predation (Webb and Welhs, 1986). It is possible that a fish's body shape alters with growth due to predation and habitat pressures. A shallower fish would be able to escape predation faster and would be able to inhabit a larger range of habitats. All species studied inhabit costal benthic habitats, so having a greater maneuverability would be advantageous with growth. This could explain the results found in all five species of a streamlined overall body shape. However even though these bulbous fishes studied are relatively dorsoventrally compressed with elongate tapering bodies, they still have large wide heads that creates larger drag. This could be an evolutionary characteristic due to predator prey

pressures. Fish with wide heads lower their risk of predation from gape-limited predators. Gape-limited predators consume their prey whole, thus the maximum size of potential prey is limited by measurement of the head (Nilsson and Bronmark ,2000). This results in a selective pressure for a wider head in order to decrease predation from gape-limited predators.

One variable that was not factored into our research was sex-specific body shape relating to growth. The sex was not recorded for individuals measured, which could have changed the way we interpreted our data. Female and males have been known to have separate rates of growth in some species of fish, for example the zebra fish (McHenry and Lauder, 2006). Further research could include examining the growth rate and body shape differences between sexes of same species.

How does body stiffness change during growth?

The second moment of area is a predictor of structural stiffness of an object. We measured cross sections along the body of to see how structural stiffness changes from head to caudal peduncle. In all species measured there was a highly similar trend of second moment of area along the body. Despite standard length differences, we found the greatest second moment of area was around twenty percent of the standard body length (Fig. 6), which was the head section of the fish. This tells us that in the bulbous species tested the stiffest part of their body is the head, also where they are the widest. Stiffness decreased dramatically from the head to the body. The standard length of the fish dictated the slope at which stiffness decreased along the body, a longer fish had a larger decrease of stiffness than a shorter fish. Maximum stiffness is concentrated in the head region while the rest of the body is relatively low stiffness in the species studied.

Our results show significant correlation between second moment of area (aka stiffness) and ontogeny. As the species measured grew in standard length their maximum stiffness along the body increases. These results do not agree with our original hypothesis, we conjectured that the stiffness would remain constant with ontogeny. Our data agrees with previous research done with aquatic vertebrate second moment of area where stiffness increased with total length (Porter et al., 2009). Body stiffness mediates swimming performance and speed by controlling the mechanical rate of working and changing shape and speed of the traveling waves (McHenry and Long, 2006). In previous research a three-fold increase of stiffness resulted in doubling of acceleration in tadpole shaped robots (Long et al., 2011). This could all imply that as fish increase in length and overall stiffness their swimming performance and ability to accelerate increases as well. This would have important implications for predator and prey interactions. A fish that is capable of faster acceleration would be a more advantageous predator and as well as a defended potential prey. With increasing stiffness a fish can accomplish faster speeds and higher maximum swimming acceleration that would help improve overall swimming performance (Long et al., 2011). It is advantageous for fish to increase in maximum stiffness with increasing length.

While we calculated the overall structural stiffness of the organism there were other variables that we did not include. True structural stiffness of fish accounts for variables such as; skin, muscle, vertebra and fins. While we did not measure these components, for the context of our research our calculations suffice as a good measurement of stiffness. Further studies could take these variables of structural stiffness into account and compare findings.

How do morphological changes during growth compare between species?

Our results show a significant difference of the rate at which second moment of area and aspect ratio decreases along the body between species (Fig. 7). This agreed with our original hypothesis, we conjectured that since we were measuring similarly shaped fish then the slope of change along the body would be comparable but not the same. Our results agree with previous studies comparing similar species that found while salmonids were similar taxa they develop at different rates and mature to different sizes (Hale, 1999). While morphological changes were comparable between species there was a distinct difference. This could help explain why there are distinct growth patterns along the body per species studied. However when looking at the similar tadpole shaped fish the pattern of body streamlining and stiffness was comparable (Fig. 5).

Growth of form and function in bulbous fishes locomotion

Our data showed similar body morphometric trends between bulbous shaped species. This could be due to their shared similar habitats, mainly encompassing benthic intertidal areas. Species tend to develop specific morphological traits to optimally utilize their environment. Different body shapes are most efficient at different stages of age in order for the fish to have high performance (Webb, 1984). When attempting to understand the reasoning of fish morphology patterns there are many variables to consider. Small changes in morphology can lead to large consequences in morphology while other larger changes may make little difference. The effect of that change can also differ with respect to the fish's habitat, size, shape and stiffness. There can be many misconceptions when understanding quantitative morphology since there are so many

factors influencing body shape (Koehl, 1996). The morphology of the tadpole shaped fish directly impacts their swimming ability and is correlated to their ability to exploit new resources and habitats. The environment in turn influences the species phenotypes and body shapes, creating a feedback loop (Webb, 1984). While we were not including all variables of body morphology, what patterns we saw can potentially give researchers insight of form and function of these bulbous head species.

CONCLUSION

The question of “why do fish body shapes vary with growth?” is a very complex multivariable subject. However, by looking at fish’s body streamlining and structural stiffness we can acquire insight into explanations behind body shape and growth. Our findings show that increasing standard length will yield increasing aspect ratios and relative stiffness along the body of individual fish. The maximum of aspect ratio and stiffness found along the body per fish was always in the head region. Increased stiffness and overall streamlining are advantageous and help increase swimming performance that could potentially be advantageous for fish’s survival.

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FIGURES

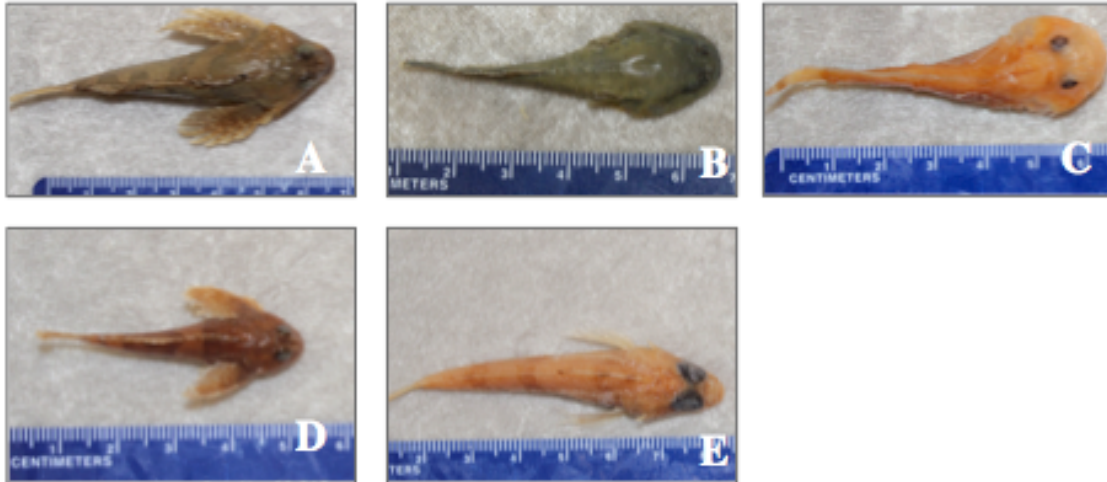


Fig. 1. Photos of all five species examined in this study; (A) *Oligocottus maculosus*; (B) *Gobiesox maeandricus*; (C) *Liparis dennyi*; (D) *Clinocottus globiceps*; (E) *Chitonotus pugetensis*. All specimens were preserved from Friday Harbor Labs Fish Collection.

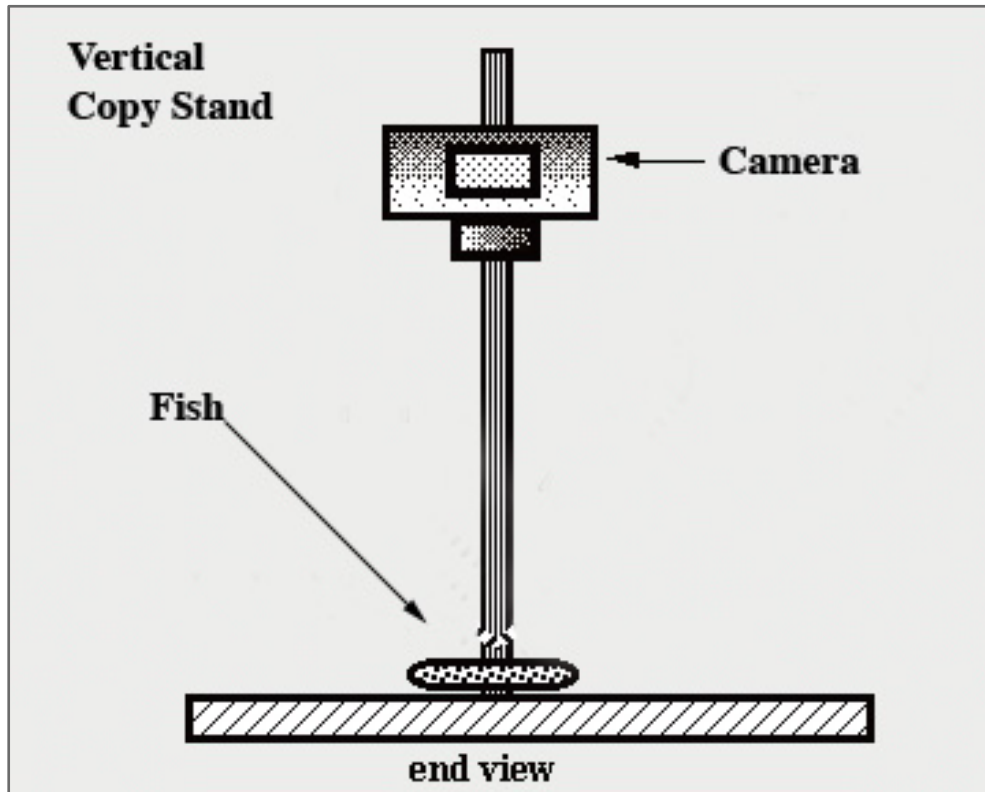


Fig. 2. Schematic illustration of experimental set up. Standardized vertical copy stand was uniform for all specimens photographed. All photos were taken with a Cannon Rebel EOS 2ti. Preserved fish were set against velvet to eliminate background noise.

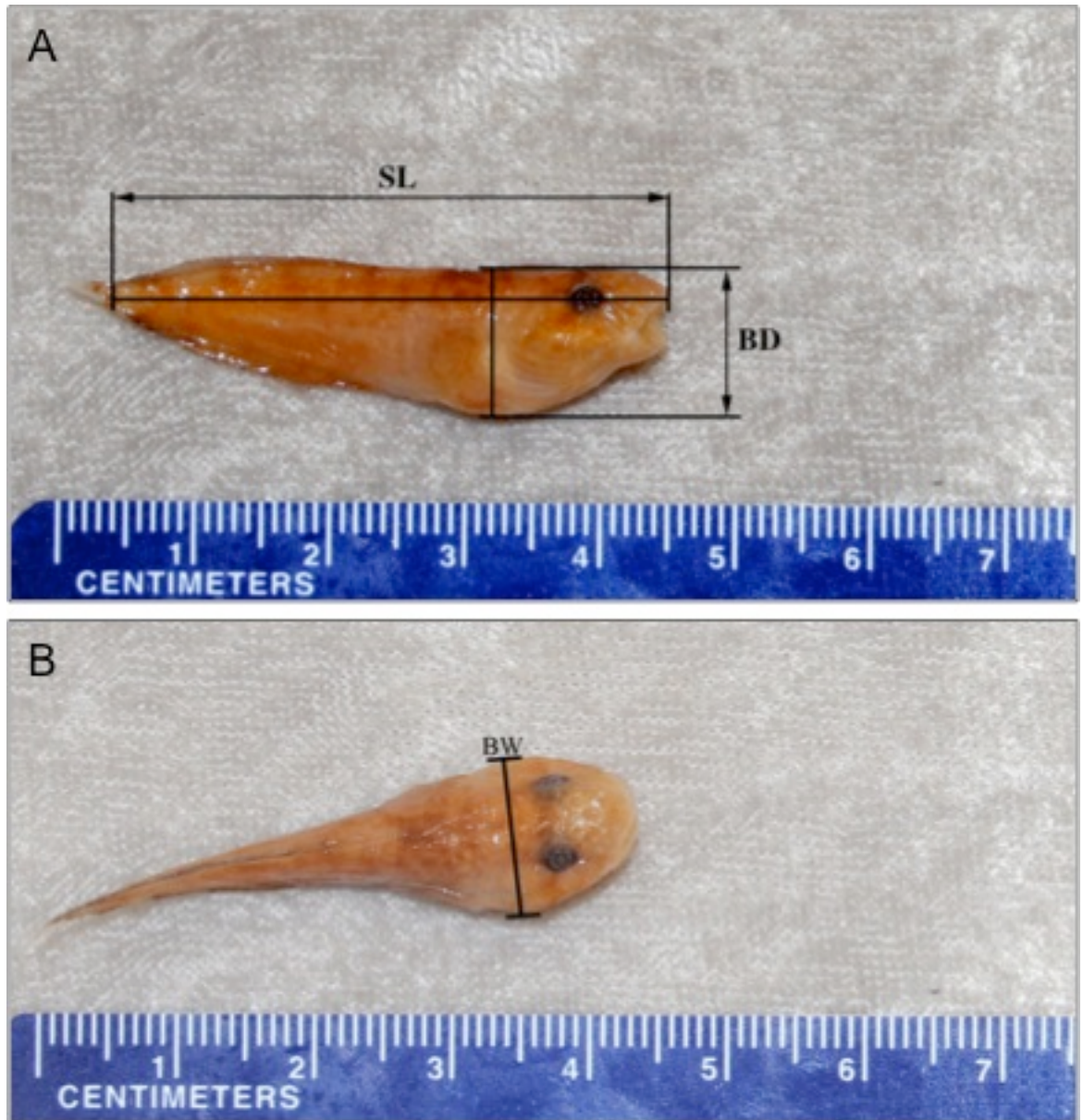


Fig. 3. Measurements of body dimensions of *L. dennyi*, in (A) lateral view and (B) dorsal view. Measurements were kept standard throughout all species and all individuals. SL, standard length (cm); BD, body depth (cm); BW, body width. BD and BW were measured at the maximum and ten percent intervals of SL along the body.

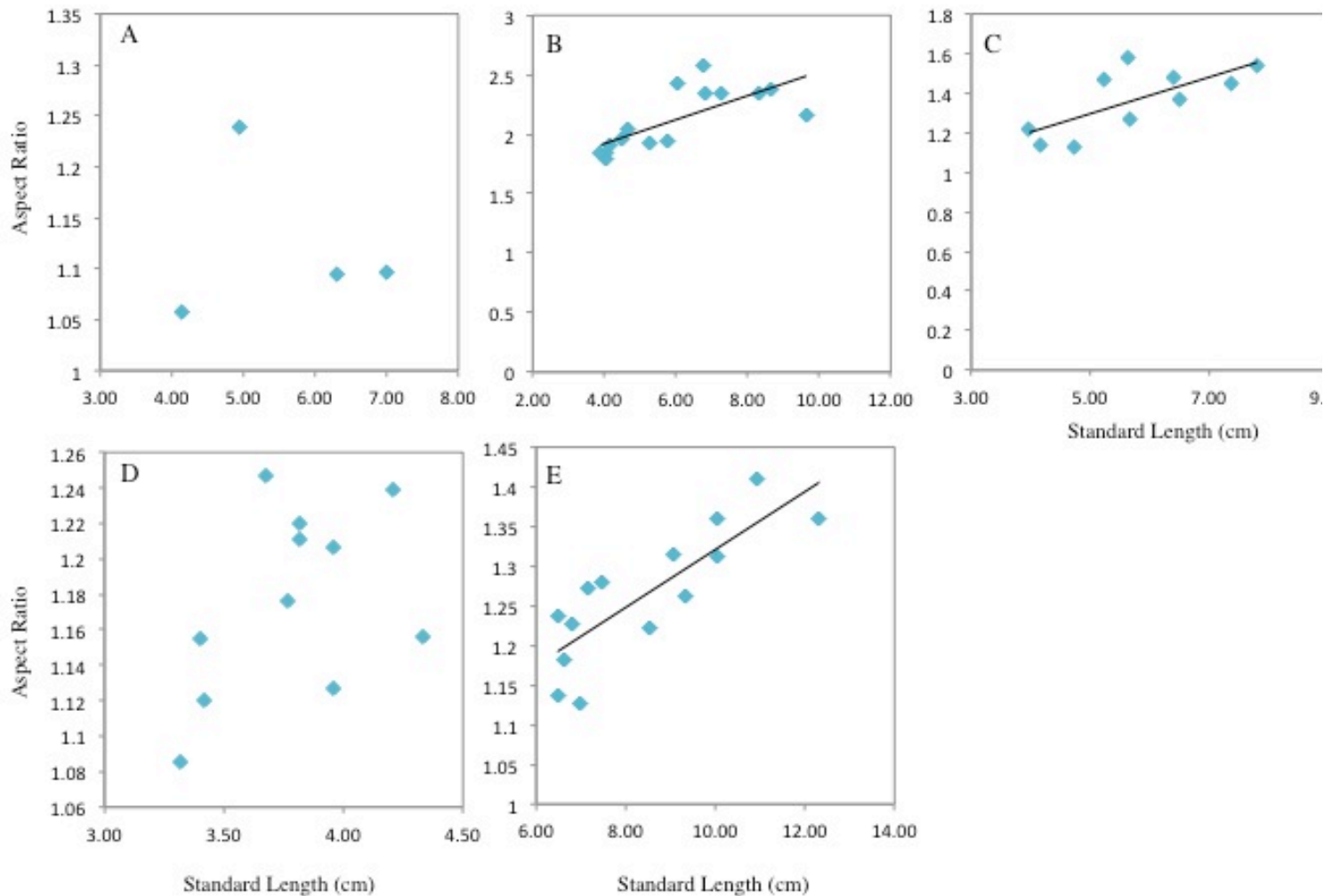


Fig. 4. Linear regression of aspect ratio (max width/max depth) over individual standard length from representative species. (B) *G. maeandricus* (Slope = 0.1, $R^2 = 0.524$; $P = 0.002$; $n=14$); (C) *L. dennyi* (Slope = 0.092, $R^2 = 0.509$; $P = 0.0205$; $n = 10$) and (E) *C. pugetensis* (Slope = 0.036, $R^2 = 0.682$; $P < 0.001$; $n=13$) were statistically significant. There is a positive correlation of overall growth to aspect ratio for these species. *O. maculosus* (A) (Slope = -0.007, $R^2 = 0.0147$; $P = 0.879$; $n=4$) and *C. globiceps* (D) (Slope = 0.046, $R^2 = 0.2078$; $P = 0.159$; $n=10$) were statistically insignificant.

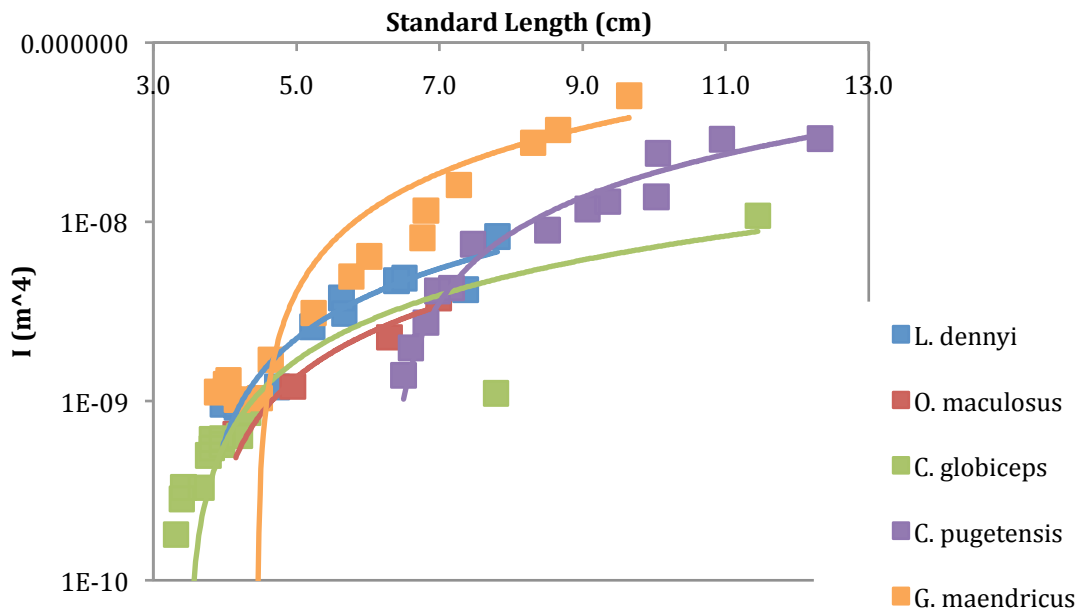


Fig. 5. Plots of maximum second moment of area (I) over individuals' standard length per species. There is a linear correlation between individuals second moment of area and their length. *O. maculosus* (Slope = 1E-09, R² = 0.94; P = 0.03); *G. maeandricus* (Slope = 7E-09, R² = 0.861; P < 0.001); *L. dennyi* (Slope = 2E-09, R² = 0.855; P < 0.001); *C. globiceps* (Slope = 5E-10, R² = 0.93; P < 0.001); *C. pugetensis* (Slope = 8E-09, R² = 0.847; P < 0.001)

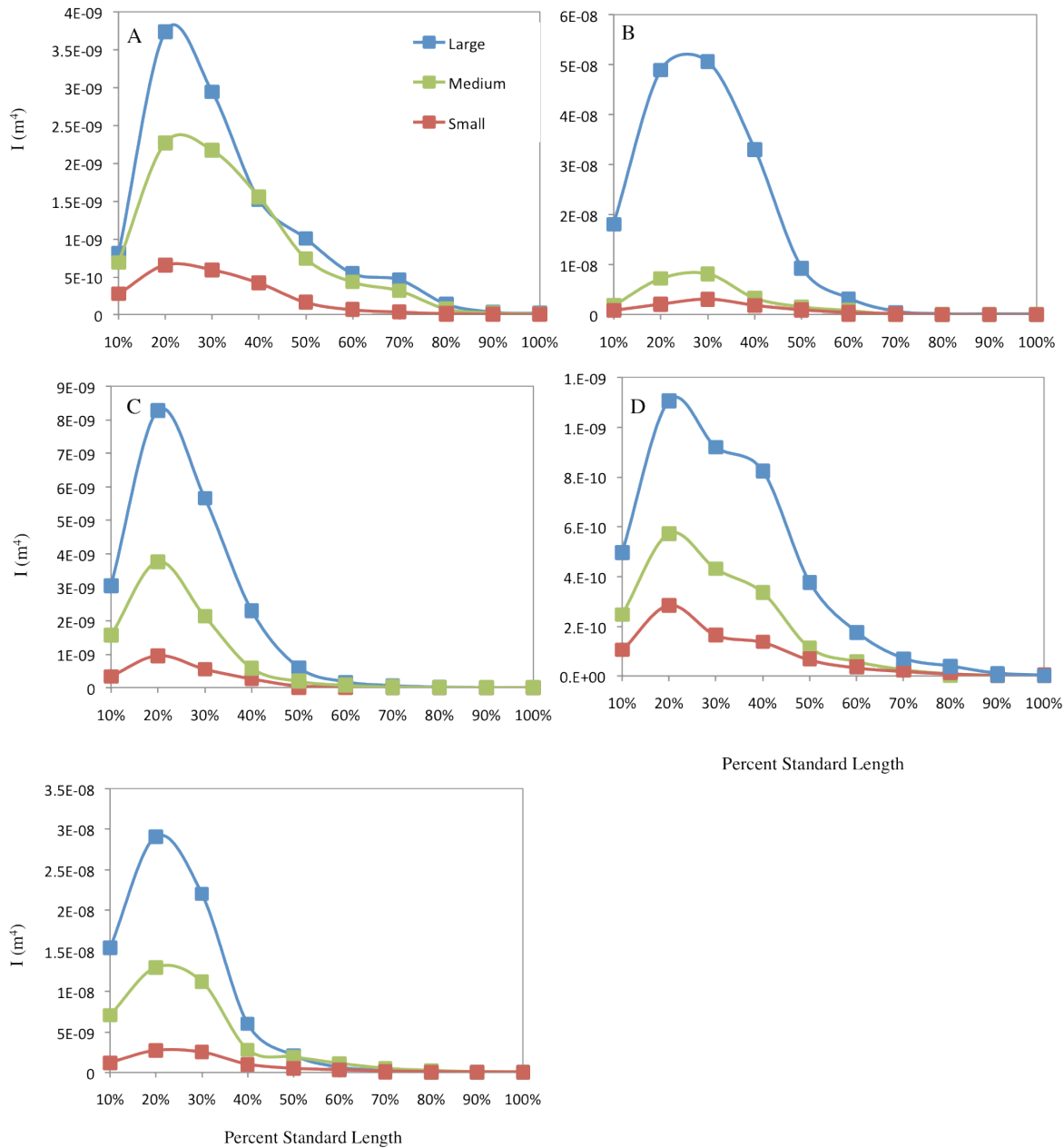


Fig. 6. Plots of second moment of area over individual standard length. For each species one large, medium and short standard length were measured. There is a visible large maximum second moment of area that varies with species but tends to be at twenty percent. With increasing standard length there is an increase in maximum second moment of area in all species. (A) *O. maculosus*, (B) *G. maeandricus*, (C) *L. dennyi*, (D) *C. globiceps*, (E) *C. pugetensis*.

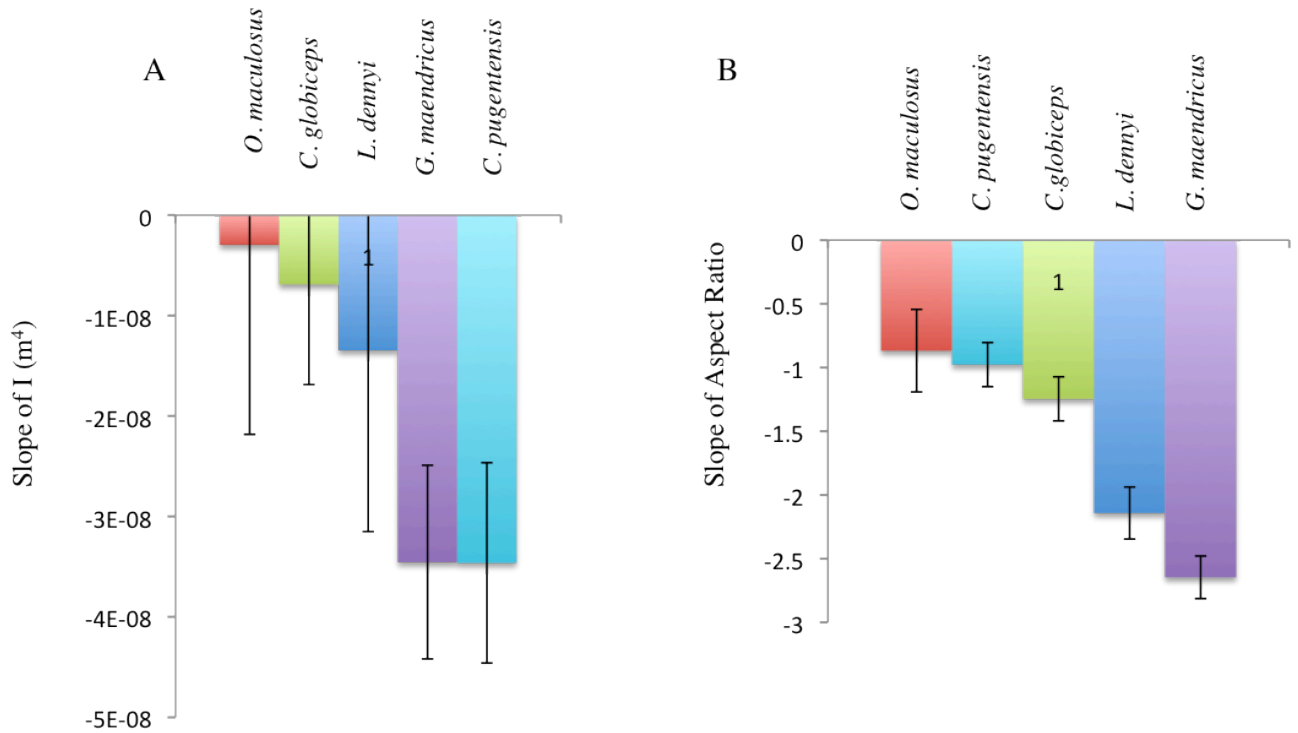


Fig. 7. Graphs illustrating degree of mean slope of (A) second moment of area, I_{SLOPE} , (B) and mean aspect ratio, AR_{SLOPE} . Slope of second moment of area (A), $R^2 = 0.1624$; $P = 0.052$, ($F_{452} = 2.521$). Slope of aspect ratio by species (B), $R^2 = 0.565$; $P < 0.001$, ($F_{452} = 16.903$). *G. maendricus* has the greatest aspect ratio slope of -2.65. *C. pugentensis* and *G. maendricus* both have the greatest slope of second moment of area.