Body Shape and Stiffness of the Scorpaeniformes of the Salish Sea

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Abstract:

The objective of this study was to examine the body morphology of a variety of Scorpaeniform fishes in the Salish Sea in order to better understand how body shape and body stiffness change along a fish's body and how they differ between closely related families of marine fishes in the same geographic location. Images were taken of 24 species in six families of Cottoidei fishes. Second moment of area, aspect ratio and fineness ratio were calculated and compared among families. Psychrolutidae had a significantly higher second moment of area than the other five families, and there were no significant differences among families for fineness ratio. Aspect ratios varied greatly among families with Psychrolutidae and Rhamphocottidae having the highest ratios, followed by Cottidae, Hemitripteridae and Liparidae, with Agonidae showing the lowest ratios. These results imply that ecology may be a better determinant in body shape and stiffness than evolution, as these closely related families showed significant variation among one another.

Introduction:

Ecomorphology is the study of how organisms are morphologically adapted to a specific niche and the ecological and evolutionary trade-offs of those specializations (Kerfoot and Shaefer, 2006). Ecomorphology combines structural, functional, ecological, behavioral and evolutionary studies in order to understand the morphologic function of an organism in its environment (Bhat, 2005). A fish's performance is the most important connection between form and ecological success. The two biggest components of form are body shape and body size. Often, small changes in shape lead to unique and innovative functions, while in other occasions a small change occurs with little or no effect on performance (Koehl, 1996). This variation in body shape and size can lead to large changes in feeding success, growth, and predator avoidance, which are directly related to fitness (Webster et al., 2011). The effect on fitness of a morphological change depends on factors such as size, shape, stiffness or habitat (Koehl, 1996).

Body shape is influenced by many factors including life history, sexual selection, predation, habitat and intraspecific and interspecific competition (Langerhans, 2008; Bronmark and Miner, 1992; Burns et al., 2009). Variation in body shape corresponding to differences in habitat and resource use is a pervasive relationship across all taxa. Body shape directly effects fitness in the form of **feeding efficiency**, swimming performance, and **susceptibility to predation** (Guill et al., 2003). **(need to add info about feeding and predation effects on morphology)**

A fish's swimming ability strongly corresponds to its prey capture, reproduction, habitat shifts and predator avoidance. Body morphology is a strong influential factor on swimming efficiency and energetic cost of transport, which in itself defines the limits of a fish's ability to consume food, and change environments (Ohlberger et al., 2006). The energetic costs of swimming depend on environmental factors such as flow velocity, and on swimming style and physiological adaptations (Ohlberger et al., 2006). These factors correspond to differences in body morphology (Hood and Heins, 2000; Pettersson and Hedenstrom, 2000; Imre et al., 2002; Guill et al., 2003).

Drag is defined as the hydrodynamic force tending to push a body in the direction of fluid movement relative to body (Koehl, 1996). Thus drag has the tendency to dislodge sessile organisms and to resist locomotion. The effect of streamlining (putting a long tapered end downstream of the body) can greatly reduce drag (Koehl, 1996). A fish with a flexible body will experience slightly less drag than a fish with a stiff body of the same shape and size due to the possible passive deformation of a flexible body into a more streamlined shape (Koehl, 1996).

The structural stiffness of a body is the mechanical property that characterizes a structure's deformation when subjected to a given external force (Long & Nipper, 1996). Some fish have the ability to alter their body stiffness by use of their muscles while swimming and can minimize the cost of bending the body by increasing body stiffness (Long & Nipper, 1996). Maximum swimming speed is increased with increased stiffness (Long & Nipper, 1996). *The stiffness of the body sets the minimum required force to drive locomotion and is therefore extremely important when looking at a fishes swimming performance*. Small changes in body shape such as streamlining can result in large changes in body stiffness (Long & Nipper, 1996).

With any change in body shape a functional trade-off develops. Body depth presents a trade-off between predation risk and swimming efficiency (Webster et al., 2011). A deep-bodied fish expends more locomotive energy through increased drag, at the same time lowering its predation risk from gape-limited predators. The opposite is true of a shallow-bodied fish. Swimming efficiency is increased due a reduction in drag, but there is also an increase in susceptibility to predation.

Compiling the many examples of variation in body shape due to water velocity, predation risk and habitat, it is likely that body shape depends on the *interactions* between predation pressures, flow regime and habitat.

The overall purpose of this study was to examine the body morphology of a variety of Scorpaeniform fishes in the Salish Sea in order to better understand how body shape and body stiffness change along a fish's body and how they differ between closely related families of marine fishes in the same geographic location. Specifically we asked how body shape changes along the length of the body and how it differs among families, as well as how structural stiffness changes along the length of the body and how it differs among families. Our hypothesis was that despite the geographic and environmental similarities, there would be a wide range of values for the body ratios and body stiffness among the families due to the diversity of niches these fishes occupy and their life history differences. For this same reason we also hypothesized that would vary significantly among families, but that it would decrease along the length of the body for all families.

Methods:

Organisms:

All of fish in this study came from the fish collection at Friday Harbor Labs. Most of the specimens had been collected from the 1950s to the 1970s in otter trawls, in and around San Juan channel in the Salish Sea. They have since been preserved in ethanol. Every member of the order Scorpaeniformes that had at least two adult specimens available was used. This resulted in 24 marine species representing the suborder Cottoidei and its two superfamilies: Cottoidea with the five families of Hemitripteridae, Rhamphocottidae, Cottidae, Psychrolutidae, and Agonidae and Cyclopteroidea with the family Liparidae (Fig. 1).

Scorpaeniformes is an order of marine and freshwater fishes with 35 families that span most of the northern hemisphere and parts of the southern hemisphere (Froese & Pauly, 2012). The synapomorphy is the presence of a suborbital stay, a spine derived from a bone below the eye that points in the posterior direction (Helfman et al., 1997). Many species are also characterized by the presence of additional spines protruding from the body, particularly the head. Most are benthic and relatively inactive. They are commonly less than 30 cm in length (Helfman et al., 1997; Froese & Pauly, 2012). Roughly 90 species inhabit in the northeast Pacific (Howe and Richardson, 1978).

Experimental Design & Data Collection:

We set up a digital camera at a 90° angle to the table surface (Fig. 2) and lay grey velvet cloth on the table to absorb light from the flash. We placed the fish on the velvet next to a ruler in order to set the scale for later photo analysis. We photographed the fish from both a dorsal view and lateral view. Using this process we took photos of the three largest specimens of each of the 24 species. We uploaded the images into the image-processing program, ImageJ, where measurements were taken. For each fish we measured the total length, standard length, maximum body depth, and maximum body width. Depth and width were also measured at each 10% interval of the standard length of the body, a value that differed with every individual (Fig. 3). We verified the total lengths of the fish with fishbase and various guidebooks to confirm each individual was an adult.

Data Analysis:

The collected data was then analyzed using Microsoft excel and the statistical program JMP. From the measurements taken from Image J we calculated aspect ratio, fineness ratio and the second moment of area as shown below:

- Aspect Ratio (AR): maximum width/standard length.
- Fineness Ratio (FR): width/depth along 10% intervals of the standard length of the body. This is a ratio of the major axis to minor axis of the body (Ohlberger et al., 2006), which measures the body slenderness, providing information about the streamlining of the fish.
- Maximum Fineness Ratio (FR_{max}): maximum value of width/depth of the 10 measurements along the length of the body.
- Second moment of area (I): $\pi/4*w^3*d$, where w is the width/2 and d is the depth/2, taken along 10% intervals of the standard length. I was calculated by approximating the cross section of the body as an ellipse, and applying it to the standard engineering equation suing the minor and major body axis's (McHenrey et al., 1995; Porter et al., 2009)). This provides a value for the structural stiffness of the body

- Maximum second moment of area ($I_{\max}$): maximum value of I of the 10 measurements along the length of the body.

These calculations were averaged for each family. We then graphed I for each family and noted where the largest slope decrease occurred. The location of the start of the slope and the end of the slope were coded (expand) and compared between families. We ran multiple univariate ANOVAs comparing family with each $I_{\max}$, $FR_{\max}$, and AR. Significant probability was set at 5% ($p<0.05$). We then graphed FR and I for each family along 10% intervals.

Results:

The average maximum second moment of area ($I_{\max}$) for each family was graphed in Fig. 4. The univariate ANOVA showed that the family Psychrolutidae was statistically significantly different from the other five families, while those remaining families showed no statistical difference between each other ($F_{5,65}=8.704$, $p<0.0001$). The average $I_{\max}$ of Psychrolutidae was 2000% greater than Agonidae, which had the lowest average $I_{\max}$, two orders of magnitude smaller. The family with the next greatest $I_{\max}$ value was Cottidae, which had a 900% difference from Psychrolutidae and a full order of magnitude smaller.

There was great variation between the average second moment of area along the standard length of the body for the six families (Fig. 7). Rhamphocottidae had the most unique I values along the body, with the fist 40% of the body increasing to its peak, then decreasing almost symmetrically to 70%, where it tailed off to close to zero at 100%

body length, the caudle peduncle. Liparidae, Agonidae and Psychrolutidae all showed similar trends, where the shape of the *I* curves follow the same pattern with a peak at 20%, decrease to 40% and a tail with very small *I* values to 100% body length. Despite these similar trends, their maximum values differed with Psychrolutidae peaking at 1.9E-7, while Agonidae and Liparidae peak near 1.0E-8, one order of magnitude lower. The shape of the *I* curve of Cottidae followed the same general trend as the previous three families mentioned, with the exception that the extremely small values did not begin until 70% body length. Hemitripteridae had a very different *I* curve, peaking at 10-20%, decreasing until 50% where it then tailed off to very low values until 100% body length. The only similarity among the six families is that from 70% onward, an area representing the posterior, or caudal region of the body, the *I* values were extremely small compared the rest of the body.

We found great significant differences between the average aspect ratio (maximum width/ standard length) among the families (Fig. 6). The AR of Agonidae was the smallest and was significantly different than the other five families, while the AR of Psychrolutidae and Rhamphocottidae were significantly different than the rest, but similar to each other, with the largest ARs. Hemitripteridae, Liparidae and Cottidae all had statistically similar ARs to each other with intermediate ARs, and statistically different than Agonidae, Psychrolutidae and Rhamphocottidae. Univariate ANOVA ($F_{5,65}$=32.226, p<0.0001).

The average maximum fineness ratio (body width/body depth) showed no statistically significant difference among the six families (Univariate ANOVA $F_{5,65}$=1.145, p=0.3458) (Fig. 5). There was a 36% difference between Liparidae, with the highest average FR_{max} and Hemitripteridae, with the lowest average FR_{max}. The fineness ratio along the standard length of the body showed variation between families. All families except Agonidae peaked in the first 30% of the body and had the lowest ratio at the caudal peduncle (100% body length). Agonidae peaked at 90% and then dropped to its lowest ratio at 100%. Liparidae had more variable ratios along the length of the body, while Cottidae and Hemitripteridae were more uniform and had almost negative linear patterns in their FR values.

Discussion:

There have been many studies on intraspecific morphological variation in fishes due to differences in flow regime, substrate type, predation risk, prey distribution and assemblage, and habitat (Webster et al., 2011; Langerhans, 2008; Kerfoot and Shaefer, 2006; Bogdanov, 2007; Pettersson and Hedenstrom, 2000). Although it is easier to make conclusions about morphological differences between populations of a species, these same general rules can be applied to species as a whole.

We hypothesized that second moment of area (I) would decrease along the length of the body for all families and that these values would vary among families. This turned out to be somewhat true. All six families were consistent in that they had higher values of I in the first 50% of the body than in the remaining 50%. McHenrey et al. (1995) found that in stiffness decreased by three orders of magnitude along the length of the body for other Scorpaeniform fishes, however I decreased only by one order of magnitude from the head to 100% body length in Psychrolutidae, while the remaining five families did not show much of a decrease from 10% to 100% body length.

The Liparidae had the lowest *I* values in the caudal region of the body. Liparidae curl their caudal region around the anterior region of the body to become more hydrodynamic and decrease drag. Their modified pelvic fins that act as a suction allow them to cling to the substrate and by curling their caudal region around their body, minimize the effect of drag and other disturbances from turbulence (Budney and Hall, 2010). This pelvic suction requires a wider pelvic surface (Budney and Hall, 2010), which by definition increases the stiffness of that region. Such suction structures are beneficial in areas of high flow velocity, however an optimal body shape for fish living in high flow zone is streamlined. The broader body shape of Liparidae most likely represents a morphological trade-off between streamlining to reduce drag, and having a wide anterior to accommodate a suction structure.

We found it interesting that the family Agonidae had the lowest *I* values among the families. Agonids are very stiff fishes that do not bend easily and have dermally derived bony plates (Ward and Brainerd, 2007). Their body shape is slender, providing little structural stiffness to the body. Porter et al. (2009) demonstrated that stiffness, and max curvature of sharks is a combination of body and vertebral morphology. Vertebral morphologies such as vertebral length, stiffness of the centra, and number of vertebrae were the biggest factors defining maximum body curvature. Our results indicate that the stiffness of their body has little impact from *I* and is more a result of either the stiffness of the vertebral column or stiffness due to their dermal plates, or a combination of both. This contribution of stiffness outside of body shape allows Agonids to remain slender in order to fit under rocks or in crevices (Froese and Pauly, 2012), which in turn allows them to hide from predators and ambush prey.

Our hypothesis that the fineness ratio (FR) would vary significantly among families was somewhat true. While there were no significant differences among the families in maximum FR, FR varied greatly among families as well as along the length of the body within each family. Cottidae, Hemitripteridae, Agonidae, Psychrolutidae and Rhamphocottidae all showed a significant decrease in FR at 100% of the standard body length, signifying that for these fishes the caudal peduncle is deeper than it is wide. Since most are sub-carangiform and esociform swimmers that use their entire caudal region to generate thrust when swimming, this decrease towards the end of the body would increase their swimming performance (Helfman et al., 1987). Thrust is maximized when the caudal region is deepest (Webb, 1978; 1982), meaning that thrust is most dependent upon the caudal region than other parts of the body. Thus, a deep caudal region is common in acceleration specialists, whereas depth along the length of the body is common in maneuvering specialist, while depth in the middle of the body is common in escape specialists (Walker, 1997).

Changes in body stiffness control swimming speed. Select fish can alter their body stiffness, which would change hydrodynamic drag on body and increase swimming efficiency (McHenry et al, 1995). Likewise, to reduce energy expenditure, a streamline body shape makes for more efficient swimming by reducing drag (Vogel 1981). The energetic costs of swimming are positively correlated to speed and size, as drag increases with increasing speed and increased surface area and energy is required to produce thrust to overcome drag (Ohlberger et al., 2006). The goal of fishes is to reduce hydrodynamic resistance, decreasing the amount of required energy during locomotion, by changes in their body shape. A fish with a low drag body shape has the ability to swim at various speeds without heavy increases in cost of transport, whereas fish with a high drag body shape experience large increases in energetic costs from small increases in swimming speed (Petterson and Hedenstrom 2000). Deep body morphology corresponds to increased energy expenditure during swimming, a direct cost of fitness (Pettersson and Hedenstrom, 2000). A pelagic fish would benefit from having a streamlined body because of their need to travel longer distances for food (Webb 1984). In contrast, fish foraging in highly vegetated areas where prey tend to be cryptic, good maneuverability is most important, which requires a deeper body. Svanback and Eklov (2003) found that perch living in littoral and pelagic zone have different body morphologies, with pelagic individuals being more streamlined than individuals living in the littoral zones. This implies a functional trade-off between body form and ecological performance, in this case between foraging ability and body streamlining.

The vast significant differences we found between average aspect ratios (AR) of the families were expected. The bulbous head regions of Psychrolutidae and Rhamphocottidae gave these families a much higher AR than the others. These fishes often live in intertidal environments that can have high levels of turbulence. Better maneuverability, defined by quick and precise locomotion including acceleration, braking, turning, hovering, etc., is important for these fish to maintain themselves in highly turbulent waters (Helfman et al., 1997). Maneuverability is thus an important mechanism for increasing foraging success and avoiding predation in structurally complex habitats (Walker, 1997; Burns et al, 2009; Moody et al., 1983). This is found in broad, deep-bodied fish, as compared to more streamlined, shallow-bodied fish (Walker, 1997). Turning radius depends on axial flexibiltiy, turning kinematics and body shape.

Fish with deep and laterally compressed bodies have greater manoeverability due to increased turning curavatue than fish with shallow, broad bodies (Walker, 1997).

The species involved in this study were mostly small fishes with high predation rates (Froese and Pauly, 2012). The need for rapid escape is therefore high. Their general body shape is not designed for fast and steady swimming. Instead they need to have good maneuverability and quick starts in order to successfully escape predators. Likewise, when food is patchy, fish with low drag will be able to forage more efficiently (Pettersson and Hedenstrom, 2000). Bronmark and Miner (1992) showed that carp with high food availability had slightly deeper bodies than carp with low food availability due to their more efficient maneuvering.

Bhat (2005) found a positive correlation between head depth and standard length, likely due to the fact that larger fish feed on larger prey and thus require deeper head sizes. Possesing a wide or a deep head can also be a morphological defense reducing predation risk. Gape-limited predators consume their prey whole, thus the maximum size of potential prey is limited by the minimum measurement of the mouth and esophageal tract (Nilsson and Bronmark, 2000; Bronmark and Miner, 1992). Furthermore, even if prey have not reached that maximum size, having a deeper body is still beneficial due to increased prey handling time (Bronmark and Miner, 1992). Because of this, predators tend to prefer shallow-bodied prey to deep-bodied prey (Webster et al., 2011). Bronmark and Miner (1992) found that the presence of a gape-limited predator led to a large increase in carp body depth. This results in a strong selective pressure for a shallow body in order to decrease predation from gape-limited predators as well as a trade-off with hydrodynamic drag and the resultant energetic loss of locomotion

Phenotypic variation can often be predicted by flow regime (Langerhans, 2008). As flow velocity increases, so does the drag experienced by the fish. The fish must somehow overcome this increased drag by steady swimming or moving to a new environment. In low flow velocity environments, conserving energy by steady locomotion is less necessary so selection favors alterative locomotion such as fasts starts, maneuvering, etc. (Langerhans, 2008).

Guill et al. (2003) discovered that different species of perch showed variation in body shape depending on the flow regime in their habitat. There was a strong association with deep-bodied perch with deep caudal peduncles living in higher flow velocities, and with shallow-bodied perch inhabiting benthic pools with low flow velocities. Similarly, the body shape of *cottus* species found in deeper, slower and siltier streams had larger heads, deep and wide bodies and wide caudal peduncles, while those living in shallow, fast flowing streams had deeper caudal peduncles (Kerfoot and Shaefer, 2006). These separate populations had morphologies that optimized their performance in each habitat. This relationship between body depth and hydrodynamic drag can be found across many populations of species (Webster et al., 2011; Bogdanov, 2007; Imre et al., 2002; Matthews, 1985; Robinson et al., 1996; Collin and Fumagalli, 2001). The same can be inferred about the six families involved in this study. Hemitripteridae, Liparidae and Cottidae had intermediate AR values that could be a way of decreasing drag in the highly turbulent environments they reside, while Agonidae had the lowest AR, optimizing its body shape for the niche it occupies.

Conclusion:

The fishes measured in this study are all known to be closely related. Each family involved is in the suborder Cottoidei and all but Liparidae are in the superfamily Cottoidea, however the specific phylogenetic relationships within Cottidae are under debate. In order to determine how much phylogeny corresponds with body morphology, it would be helpful to have resolved phylogenetic relationships. Meanwhile, because of the known phylogenetic relationships between these study organisms and the variation in body morphology it is clear that body morphology is not the best determinant in evolutionary trends.

From information gathered from this study as well as outside literature, it appears that body shape is influenced by a combination of evolutionary trends, habitat, and interspecific and intraspecific interactions, and because the relationship between a fish and its environment is always changing, the relationship between body shape and body stiffness and ecology is dynamic.

Further research:

In order to figure out the true stiffness of these fishes further research could be done to measure the second moment of area of the vertebra centra to calculate the structural stiffness of the vertebrae, as well as any additional stiffness contributed by the skin and any dermal plates, bones or spines. These could be quantified and the percent contribution of each factor determined. The active increase of stiffness via muscle work could also be analyzed.

It would also be useful to know the specific flow regimes and specialized niches of the study fishes by examining the specific habitats the study fish occupy, as well as their role in the food web. Knowing what flow regime the fish lives in and what kinds of predators it is trying to avoid could provide insight into why their body is shaped a certain way.

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Figures:

Family:	**Species:**
Agonidae	*Odontopyxis trispinosa*
Agonidae	*Agonus emmelane*
Agonidae	*Podothecus accipenserinus*
Agonidae	*Xeneretmus latifrons*
Agonidae	*Bathyagonus nigripinnis*
Liparidae	*Liparis pulchellus*
Liparidae	*Liparis dennyi*
Liparidae	*Liparis rutteri*
Liparidae	*Liparis fucensis*
Liparidae	*Liparis florae*
Hemitripteridae	*Blepsias cirrhosus*
Psychrolutidae	*Dasycottus setiger*
Psychrolutidae	*Phychrolutes paradoxus*
Rhamphocottidae	*Rhamphocottus richardsonii*
Cottidae	*Ascelichthys rhodorus*
Cottidae	*Artedius fenestralis*
Cottidae	*Artedius harringtoni*
Cottidae	*Oligocottus snyderi*
Cottidae	*Oligocottus maculosus*
Cottidae	*Leptocottus armatus*
Cottidae	*Triglops pingeli*
Cottidae	*Clinocottus globiceps*
Cottidae	*Radulinus asprellus*
Cottidae	*Chitonotus pugetensis*

Fig. 1: List of families and species measured. Total of 24 species in six families from the order Scorpaeniformes. Agonidae, n=16; Liparidae, n=14; Hemitripteridae, n=3; Psychrolutidae, n=6; Rhamphocottidae, n=2; Cottidae, n=30.

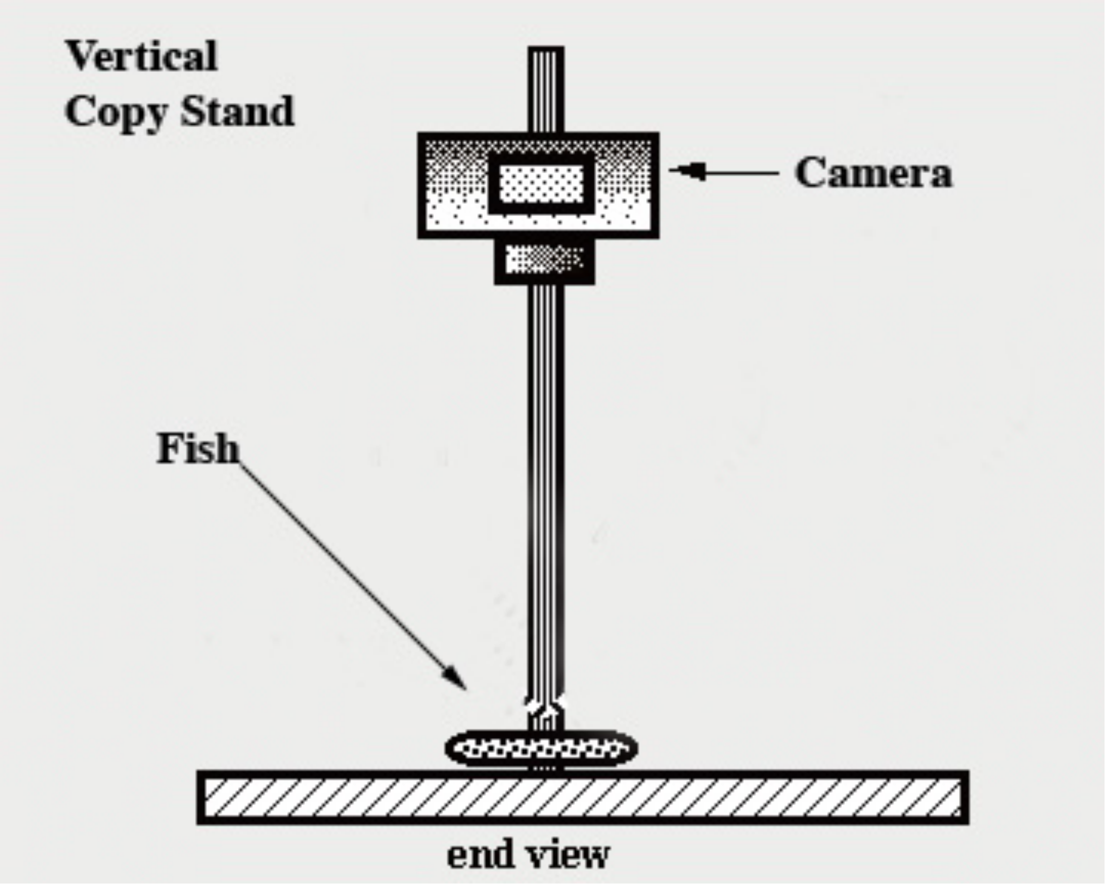

Fig. 2: Photography set-up. Individual fish photographed alongside a ruler for scale. Camera pointed at 90° to table surface. Each fish photographed on the dorsal and lateral side.

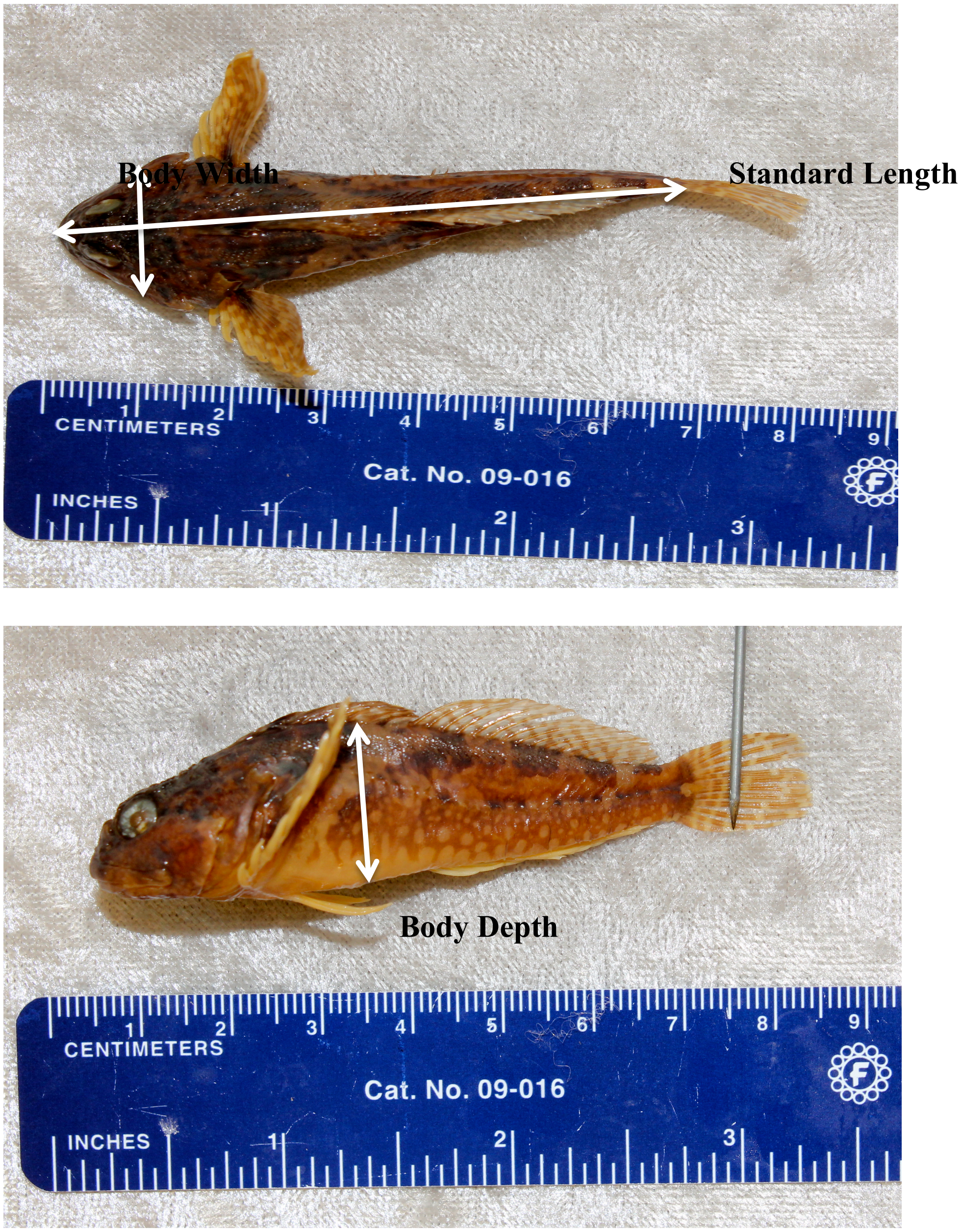

Fig. 3: Morphological measurements of fish. Standard length measured from tip of snout to the caudal peduncle. Body width measured in 10% intervals of standard length. Body depth measured from dorsal line to ventral line in 10% intervals of standard length. Maximum body width and body depth also measured. All measurements exclude fins, spines, cirri and other body protrusions.

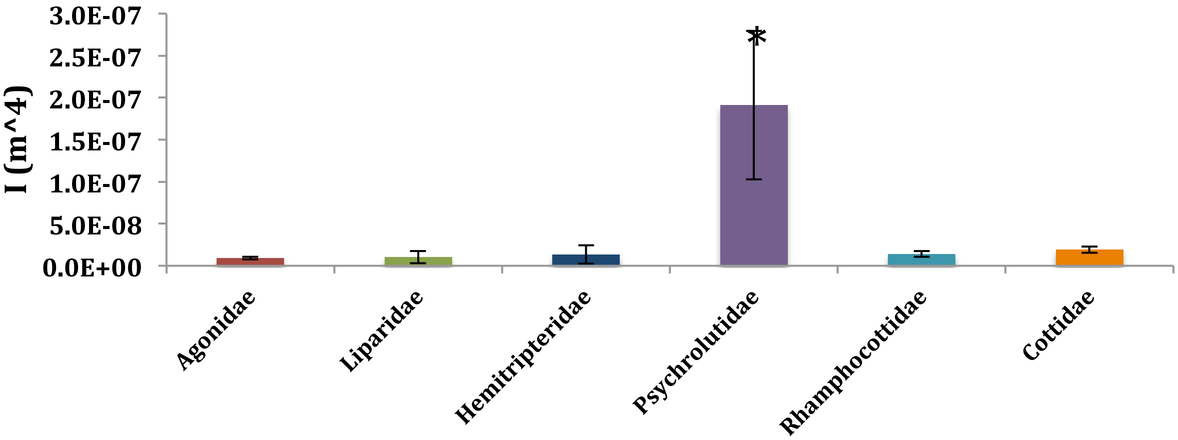

Fig. 4: Average maximum second moment of area (*I*) for each family showing standard error of the mean in error bars. *I* is defined as $\pi/4*w^3*d$, where w is the body width/2 and d is the body depth/2. Maximum *I* was chosen based on the highest values of *I* taken in 10% intervals along the standard length of the body. The star above Psychrolutidae denotes a significant difference from the five other families found in a univariate ANOVA ($F_{5,65}$=8.704, $p<0.0001$).