

**Kinematic Effects on Schooling in Juvenile *Rachycentron canadum***

An essay submitted in partial fulfillment of  
the requirements for graduation from the

**Honors College at the College of Charleston**

with a Bachelor of Science in

Marine Biology

Sarah Kate Shore

May 2017

Advisor: Eric McElroy

## INTRODUCTION

Many animals exhibit social grouping behaviors, the motivations for which can be grouped into four broad categories according to benefits that grouping may provide. These categories are social/genetic, anti-predator, enhanced foraging, and energetic benefit motivations. While in certain contexts there may be drawbacks to grouping, such as aggression among group members (Krause and Ruxton 2002), parasitism (Poulin 1999), and an occasional increased risk of predation (Krause and Godin 1995), for many animals it appears that the benefits outweigh the risks. This study looked at the potential energetic benefit that cobia receive by swimming in a group.

The social/genetic aspect of group behavior is apparent in animals that group together to find mates or for the calming benefit of being around conspecifics. In fishes, herring have been shown to exhibit a strong stress response to being isolated from their school (Partridge et al. 1980). For instance, one study showed that when blackchin shiners were removed from their school, they had a higher rate of respiration which may indicate stress (Abrahams and Colgan, 1985). Apart from increasing chances of finding a mate, this paper implies that group behavior may be physiologically used as a stress reduction mechanism. Swimming in schools may also have an effect on the growth rate of fishes (Davis and Olla, 1992) and improve the accuracy of homing and migration (Larkin and Walton, 1969; Pitcher and Parrish, 1993).

Several hypotheses have been proposed to explain why large group formation in animals such as fish and birds works as an anti-predator response. The first of these theories is the “predator confusion effect,” first proposed by Milinski and Heller in 1978. This effect occurs when a predator is unable to pick out a single individual as prey because the size and movement of the group overloads the predator’s visual senses. This finding has been demonstrated both

experimentally and with computer models (Iaonnu, Tosh, Krause 2008). The second hypothesis on the effectiveness of group predator avoidance is the “many eyes” hypothesis (Olsen, 1964, Eggers, 1976). Unlike the predator confusion hypothesis, the many-eyes hypothesis describes the advantage of the prey group’s many-eyed ability to scan the environment for threats. With an increase in group size, the prey can decrease their individual predator scanning and rely on a higher chance that the group as a whole will spot a predator. This likely increases individual foraging time (Olsen et al. 2015).

The last hypothesis for an anti-predatory benefit to grouping is the “encounter dilution” effect. Turner and Pitcher characterized this theory as a combination of detection and attack probabilities. The detection component assumes that a predator is less likely to encounter a single aggregation of conspecifics than a scattered solitary distribution of the same number of conspecifics. The attack probability assumes that a predator is more likely to attack a solitary animal than a group of the same animal. Essentially, an animal would have a probabilistic advantage in a group due to the decreased likelihood that a predator would encounter the group and then attack it (Turner and Pitcher 1986).

On the other side of the predator-prey equation, being in a group often leads to enhanced foraging opportunities. This is apparent in tertiary predators such as dolphins, who use group strategies to locate and capture prey. While group cooperation to catch prey is more obvious in animals such as cetaceans, other animals have demonstrated group foraging ability. Aerial photographs of Atlantic bluefin tuna have shown the fish swimming in a parabolic shape, suggesting an intentional cooperative hunting strategy (Partridge and Kalish 1983). Additionally, Pitcher et al showed that multiple species of shoaling cyprinid fishes had a statistically significant decrease in the amount of time it takes to find a patch of food as group size increased

(Pitcher, Magurran, Winfield 1983). The results of this study are not necessarily evidence of coordinated hunting, but they show the foraging advantage that being in a group can bring.

Lastly, alongside mating, predator avoidance, and increased foraging motivation, there may be a significant energy benefit to moving in a group. This applies to many groups of animals; for instance one study found that the energy expenditure of ducklings is decreased when swimming in a line (Fish 1995). In fishes, it is theorized that trailing individuals in a school can take advantage of the reverse von Karman street vortices shed from the front fish in order to decrease their energy expenditure (Weihs 1973, Liao et al. 2003a). This model requires that the fish swim diagonally behind each other, however, studies on virtual schools have shown that fish swimming behind each other and in rectangular or diamond shapes could have an energy advantage over fish swimming alone (Hemelrijk et al. 2014). Another implication is that as fish swim at increasing speeds, front fish will shift backward and become trailing fish in order to rest in the von Karman street vortices of the new leaders (Killen et al. 2012). It is assumed that the leaders of fish schools experience the same energy expenditure of fish swimming alone (Weihs 1973, Herskin and Steffensen 1998). This study aims to explore the energetic benefit hypothesis by testing whether fish in the front of a four-fish juvenile cobia school have a higher tail-beat frequency and larger tail stroke amplitude, and therefore a higher energy expenditure than fish the in middle or back of the school.

The fish used in this study are *Rachycentron canadum*, commonly called cobia. Cobia are a species of fast-growing subtropical and tropical marine fish. Found worldwide in temperate and tropical oceans, excluding the eastern Pacific, cobia are a popular sports fish and are also grown in aquaculture for the seafood market. The maximum recorded size of cobia is 200 cm, while typical adult lengths are around 110 cm. Their typical recorded weight is 68 kg (Froese and Luna,

FishBase). Cobia are found over a variety of habitats, including rocky, muddy, or reef bottoms. They frequent both inshore pilings and offshore buoys. Due to their solitary adult nature, there is not an established wild cobia fishery. However, groups of adults are known to form and follow large pelagic fishes (Froese and Luna, FishBase). Cobia occur in South Carolina nearshore waters from April through October, moving offshore and southward as water temperatures drop in the fall. Cobia presence peaks in late spring, after which larger individuals move offshore and are replaced by younger individuals. The South Carolina Department of Natural Resources identifies degradation of inshore habitats, the potential for overfishing, and a lack of knowledge about spawning, larval, and juvenile habitats as conservation concerns (Hammond 2001).

### Taxonomy and Morphology

Cobia are the only representative of the family Rachycentridae. They are members of the large fish order Perciformes, meaning “perch-like fishes.” Perciformes is a vast order that encompasses 156 families from tiny Blenniidae and Gobiidae species to cichlids, snappers, wrasses, and scombrids such as tuna. Cobia as a singular cosmopolitan species is defined by 7-9 dorsal spines not connected by a membrane along with a darkly pigmented body, dorsally compressed head, and lunate caudal fin in adults. Cobia bear a strong resemblance to the family Echeneidae, or the remora family. Juvenile cobia have rounded caudal fins and are generally elongated compared to the stockier bodies of adults. As cobia mature, the caudal fin becomes deeply forked or lunate (Froese and Luna, FishBase). Cobia mature in two to three years, with males reaching about 60 cm and females reaching around 77 cm. This makes them a fast-growing fish, with a recorded lifespan of about 15 years (Hammond 2001, Froese and Luna, FishBASE).

## METHODS

### Fish Procurement and Care

In August 2016, an order for about 16-20 cobia fingerlings was placed through the South Carolina Department of Natural Resources aquaculture system. The fish came from Waddell Mariculture Center in Bluffton, South Carolina, and were from wild broodstock collected from Port Royal Sound, South Carolina. The fish were held in circular holding tank at ambient water temperature, which during the month of the experiment was at an average of 19.6°C. The seawater was from Charleston Harbor, which has an average winter salinity between 30-35 ‰. They were fed twice a day but were withheld food for 24 hours before experiment.

### Biomarking the fish

Sixteen fish were tagged using small Biomark fish tags, including a Biomark injector pre-loaded with tags. First the fish were anesthetized using 100mg/L concentration of Tricaine-S, mixed with an equal part sodium bicarbonate. This was mixed in a bucket with seawater, and the fish were placed in the bucket until they began to rotate onto their sides. They were quickly taken out and a small section of their back next to the left of the dorsal fin was sterilized with iodine before the tag injector was used to inject the barcode tag. The wound was sealed with 3M VetBond™ and the fish were placed in a recovery bucket with an airstone for about 30 minutes to make sure they regained consciousness. Fish were allowed to heal for two weeks before swimming trials. Each fish was tagged with a unique barcode identification number.

## Flume set up and swimming trials

A swimming flume was set up with Charleston harbor seawater at ambient temperature (19.2-19.9°C). The flume flow speed was calibrated using a ratio of 3.27hz/0.1 m/s flow. A tenth of a meter increments were chosen for increasing the flow speed because the fish were about 0.1 meters in length, so each increase of 0.1 m/s would be an increase of swimming one more body length per second. Fish were placed in flume in groups of four at a time and allowed to acclimate for one hour before swimming trials began. Before being placed in the flume, the fish were scanned for their biotag ID and were further identified for the trial by supergluing a small piece of fluorescent tape onto their heads. There were four tape shapes per trial: circle, half circle, square, and triangle. This differentiated the individual fish in the videos. A new set of four fish was used for each trial.

A GoPro Hero4 Black camera was mounted over the fish flume, which had an open top. After an hour to acclimate at 0.3 m/s, the flume speed was increased at 0.1 m/s intervals every ten minutes until the fish reached exhaustion. Exhaustion was defined as the fish no longer resisting the flow of the flume, and coming to a rest against the metal grate at the back of the flume swim chamber. When an individual fish reached exhaustion, the flume speed would be lowered back to 0.3 m/s briefly, and the exhausted fish would be removed and put back in the holding tank with the rest of the school. A video was started at 30 frames per second after five minutes of swimming at each new speed, capturing the last five minutes of each ten minute trial. Typically the entire experiment lasted for 50-60 minutes, with at least one fish reaching a maximum of 0.9 m/s over six ten-minute increments.

## Analysis

The GoPro videos were first trimmed by selecting a 30 second sample in the middle of each five minute video. These 30-second clips were analyzed using Argus video editing software (how do I cite this?). The D warp function was used first, in order to convert the GoPro Hero4 Black's fisheye lens view into straight angles. The Clicker function was used next to digitize the dorsal tip of the caudal fin of each fish in each video. The dots digitally marked on the tip of the fins in the videos were recorded as pixel x/y distances in a .csv file, and this distance was converted to millimeters so that amplitude and frequency could be calculated. Matlab was used to process the columns of x/y distance data, and to provide exportable vectors of amplitudes and frequencies as well as tables of summary statistics. The packages used were base, signal processing, statistics, image processing, and curve fitting. A student's t-test was run in Microsoft Excel to examine frequency and amplitude correlation strength between front, middle, and back fish groups.

## RESULTS

This study showed that a fish's school position did not have a statistically significant effect on caudal fin amplitude or frequency. Figure 2 shows that while average frequency was lower for fish in the back of the four fish school, there was not a significant difference in frequency when swimming in the front vs the back of the school. ( $t = 0.535$ ,  $df = 19.394$ ,  $p = 0.599$ ). There was also no statistically significant difference in frequency between the front fish and the middle fish ( $t = 0.271$ ,  $df = 24.196$ ,  $p = 0.789$ ). Figure 1 values show that the back fish had a wider caudal fin stroke amplitude at 67 mm average amplitude; however the difference between the back fish average amplitude and the front fish average amplitude was still not



statistically significant ( $t = 0.939$ ,  $df = 18.797$ ,  $p = 0.360$ ). The amplitude of the front fish versus the middle fish was also not statistically significant ( $t = 0.177$ ,  $df = 23.422$ ,  $p = 0.861$ ).

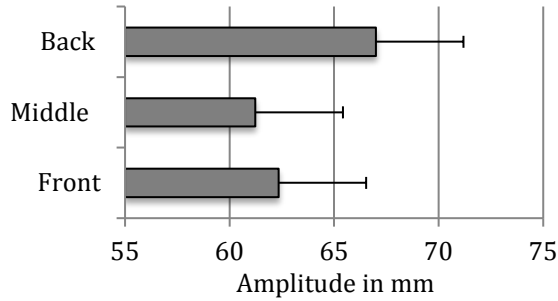


Figure 1. Amplitude of fin strokes arranged by average position of fish in four-fish school. Standard Error:  $\pm 4.186$  mm, Front  $n = 13$ , Middle  $n = 26$ , Back  $n = 10$ , T-test front amplitude vs. middle amplitude:  $p = 0.861$ , T-test middle amplitude vs. back amplitude:  $p = 0.244$ , T-test front amplitude vs. back amplitude:  $p = 0.360$

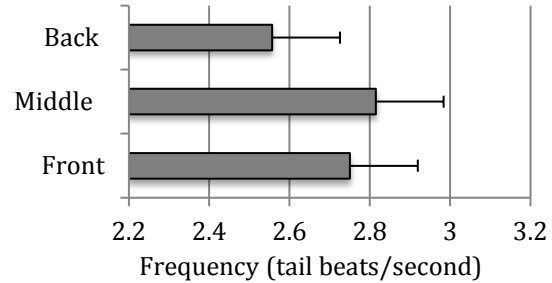


Figure 2. Frequency of caudal fin beats per second arranged by average position of fish in four-fish school. Standard error:  $\pm 0.169$  tail beats/second, Front  $n = 13$ , Middle  $n = 26$ , Back  $n = 10$ , T-test front amplitude vs. middle amplitude:  $p = 0.789$ , T-test middle amplitude vs. back amplitude:  $p = 0.408$ , T-test front amplitude vs. back amplitude:  $p = 0.599$

The percent of time spent at the front of the school did not appear to have a relationship with the  $U_{crit}$  values achieved by the fish. All fish that spent at least some portion of time at the front of the school had a  $U_{crit}$  between 0.613 m/s and 0.8 m/s, with a standard error of 0.026 m/s (Figure 3). The points displayed on Figure 3 show no trend or relationship between percentage of time at the front of the school and  $U_{crit}$ . Additionally, there was no correlation between position in school and  $U_{crit}$  even for fish that did not spend any time at the front of the school (Figure 4). The  $p$  values for student  $t$ -tests between front, middle, and back fish groups were between 0.367 and 0.734.

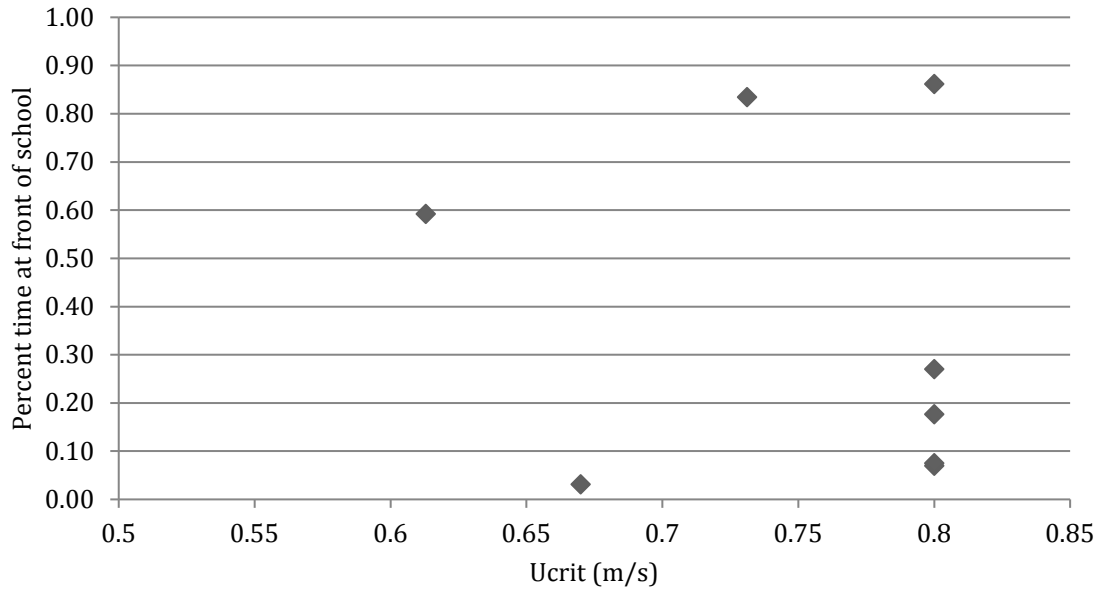


Figure 3. Percent time at front of school vs.  $U_{crit}$ . There is no relationship between the amount of time spent at the front of the school and the  $U_{crit}$  achieved by the fish.  $N=7$ , standard error = 0.026 m/s

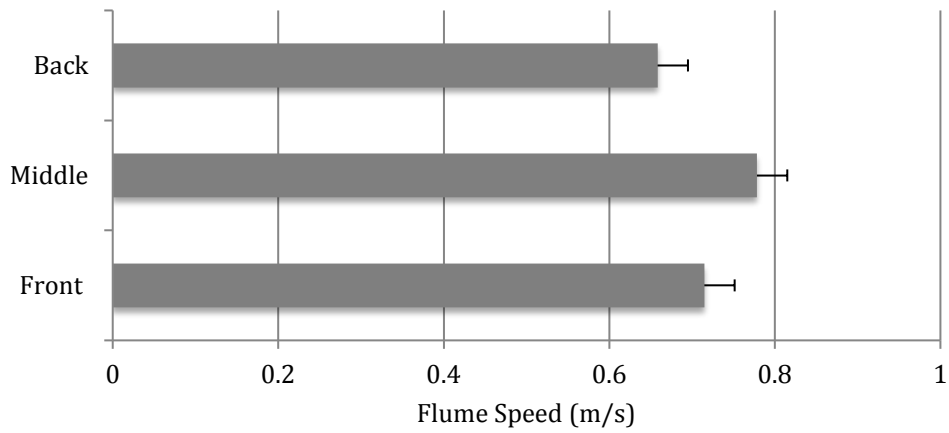


Figure 4.  $U_{crit}$  speed reached based on position in school. There is no significant difference between the average  $U_{crit}$  speeds achieved by fish in the back, middle, or front of school. Standard Error = 0.367 m/s Back fish  $n = 3$ , Middle fish  $n = 6$ , Front fish  $n = 3$ . T-test Front vs. Middle  $p$  value = 0.367, T-Test Middle vs. Back  $p$  value = 0.479, T-Test Front vs. Back  $p$  value = 0.734

Finally, the amount of times that fish switched school positions as well as the percentage of time that front fish stayed at the front seems to trend according to the speed the fish were swimming. Figures 5 and 6 show that despite weak linear correlations, the fish switched positions more often as flume speed increased from 0.3 m/s to 0.7 m/s, and spent a smaller percentage of time at the front as speed increased. Also, the  $R^2$  statistics of 0.69 and 0.53 for Figures 5 and 6, respectively, do not reach a level of significance above 0.1. The  $R^2$  value would have to be at least 0.9 to reach a significance level of 0.1 with 2 degrees of freedom ( $n = 4$ ,  $df = 4 - 2 = 2$ ).

Figures 7 and 8 reflect individual fish instead of averages at each speed (there were four speeds so there were only 4 average data points in Figures 5 and 6). The resulting graph is step-wise, which makes sense because at speed 0.3, for example, one of the trials had a fish swimming in the front 93% of the time. The other fish that spent 7% of its time in the front has a weak front percentage compared to the main leader. However, both of these points are included in Figure 7, which shows each front fish's percentage time spent at the front over each specific speed.

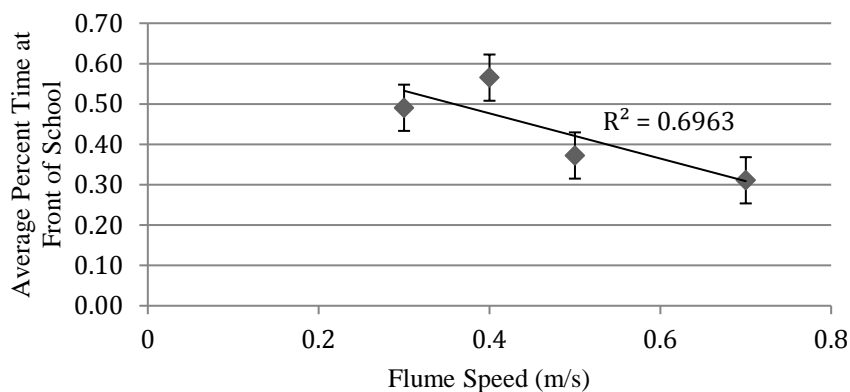


Figure 5. Percentage of time spent at front by fish as flume speed increases. There is a weak linear correlation which implies that fish spend less time at the front of the school as speed increases. Standard Error:  $\pm 0.057$

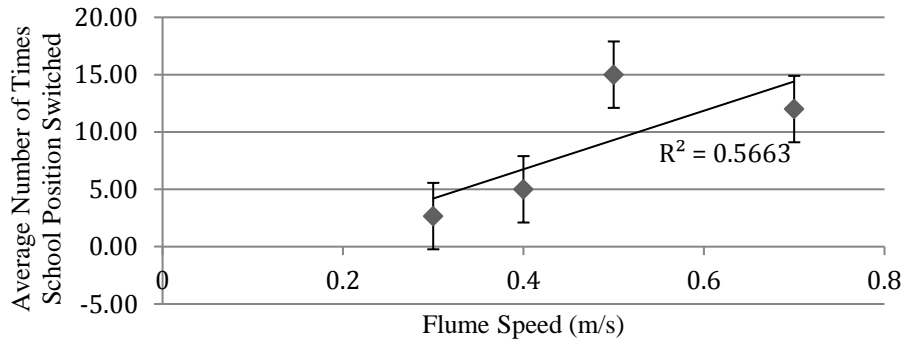


Figure 6. Average number of times school position was switched by fish at different flume speeds. There is a weak linear relationship showing that increased speeds may result in increased position changes. Standard Error:  $\pm 0.29$

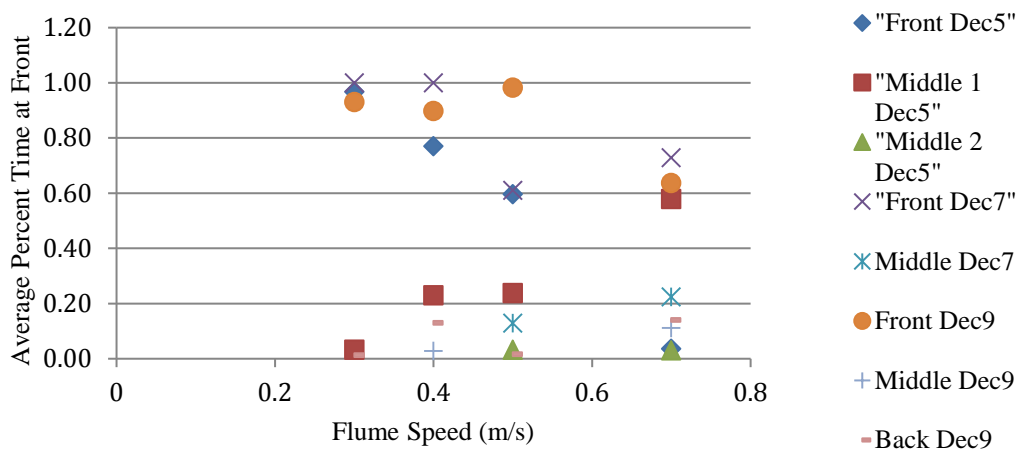


Figure 7.  $n = 26$ , the number of fish that spent at least one second at the front of the school per video. This graph is the percent of time that each of these individuals spent at the front of the school per video plotted over flume speed. It appears that the front fish start to decrease their time at the front as speed increases, while middle and back fish begin to move forward.

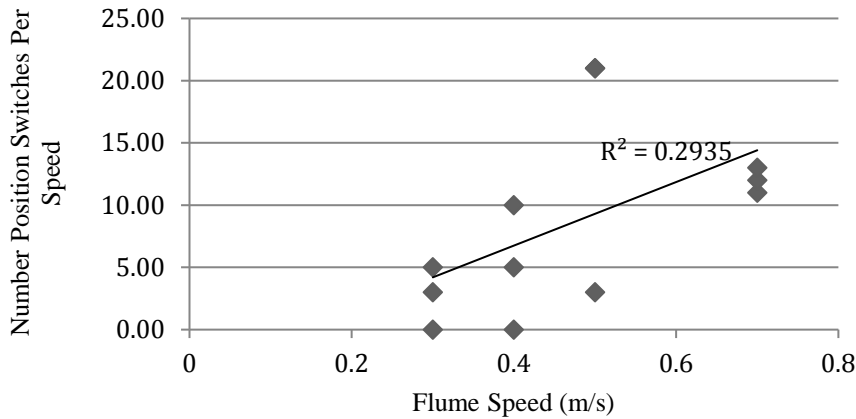


Figure 8.  $n = 11$ , the number of videos. This graph is the number of times school positions switched per video over flume speed.

## DISCUSSION

The results of this study do not support the hypothesis that fish swimming in the front of the school have a higher tail beat frequency and a wider caudal fin amplitude. If this hypothesis was supported, it would correlate with greater energy expenditure in front fish. This would show that fish schooling in the middle or back positions do not work as hard and may receive an energetic benefit for swimming behind other fish. However, the lack of statistically significant results to show this renders the hypothesis unsupported.

It appears that the results of this study are not aberrant in the literature. A paper on grey mullet (*Liza aurata*) swimming performance in schools and alone found that position in the school did not have a significant effect on the energetics of the fish in that school (Marras et al. 2015). It was only after comparison of the schooling mullet to individually swimming mullet that a difference in energy expenditure was found. All fish in a school got an energy break. This energetic saving was greatest at the lowest swimming speed, and rank from front of school was not an explanatory value in tail-beat frequency reduction according to the study's most parsimonious generalized linear mixed model (GLMM). Similar to the current study, tail-beat

amplitude in the Marras et al. study did not vary in relation to tail-beat frequency, speed, or position (Marras et al. 2015). A paper exploring swimming performance in schools of golden shiners (*Notemigonus crysoleucas*) showed that even the weakest fish in their schooling trials had a higher critical swimming speed than individuals swimming alone (Boyd and Parsons 1998). Marras et al. found that although fish saved energy by swimming in a school regardless of position, fish ahead of their neighbors used 8.8% less energy than fish swimming alone, and fish behind their neighbor used 19.4% less energy than lone fish. However, the energy expenditure differences between anterior and posterior positioned fish were not statistically significant when compared with each other (Marras et al. 2015). It seems odd that even fish swimming at the front of the school would experience an energetic advantage over fish swimming alone, which is contrary to the theoretical energy benefit hypothesis proposed by Weihs 1979. However, Marras et al. suggest that front fish may get a boost from the zone of high pressure created around the heads of the fish swimming behind them, similar to a bow-wave riding effect (Marras et al. 2015). However, the authors assert that studies employing a digital particle image velocimetry (DPIV) method must be done to test whether or not front swimming fish get a bow-wave high pressure boost from the fish behind them (Marras et al. 2015).

Marras et al. found that with increasing speed, the energetic advantage of each schooling fish relative to solitary fish decreased. Additionally, the researchers found that the fish seemed to have a harder time controlling their position relative to neighbors at high speeds (Marras et al. 2015). This current study's results show a slight increase in position switching among fish as water flow speed increased from 0.3 m/s to 0.7 m/s, aligning with Marras et al.'s results. Boyd and Parsons found that their schooling *Notemigonus crysoleucas* constantly changed positions, shifting front to back, and did not imply that the rate of position switching increased with

swimming speed. However, the occurrence of fish “mirror-image” mimicking in tail-beat frequency increased with swimming speed (Boyd and Parsons 1998).

In order to go forward with the current study, it would be beneficial to run more schooling trials in order to see if significant results would come out of an increased sample size of front, middle, and back fish position observations. Additionally, it would be interesting to conduct this experiment while swimming fish individually, in order to test whether individual juvenile cobia have poorer swimming performance alone. Individual variables such as oxygen uptake in a respirometer could be examined to predict how well an individual fish may do in a schooling scenario.

At the end of their study, Marras et al. asks the question of whether some fish have a propensity to lead due to physiological or personality differences. Neither Marras et al., Boyd and Parsons, nor this current study swam the same fish more than once. It would be possible to make a school of the three leading fish of this study’s trials, and swim them to determine which one shows the highest propensity to stay in the front position. These “leader” individuals could also be swam with fish from other positions in this study, in order to see if some fish really are school leaders. The same schools used in this study could be run again, this time at a later date after the fish have grown. This would offer a look at whether or not fish have a tendency to choose front, middle, or back school positions across several months of growth. If so, it would be interesting to further examine whether or not front leading fish showed a significant difference in body proportion compared to others in the school.

Overall, cobia may or may not energetically benefit from swimming in schools, although the results of Marras et al. and Boyd and Parsons suggest that they do. The motive behind schooling in cobia is probably an intersection of several factors. As fingerlings and juveniles,

cobia likely school to avoid predation. As larger adults, cobia have been known to school around larger pelagics such as sharks and rays (Hammond 2001). This may be beneficial for foraging. For example, if cobia are following a macrocarnivore shark, they may be able to eat residual pieces of the shark's prey. However, this does not explain why they would school around planktivores such as whale sharks and manta rays. In these scenarios, it is likely an energetic benefit of moving in the wake of a large swimmer or still the benefit of predator avoidance that drives this behavior.

While the questions behind this research are driven by the desire to find an answer to why cobia school, it is always possible that schooling in cobia is non-adaptive or vestigial. Cobia bear a strong morphological resemblance to remoras and it is likely that these two families, *Rachycentridae* and *Echeneidae*, share a recent common ancestor among teleost perciform fishes. Remoras have adapted to literally stick on to the large fish that they follow, utilizing a suction disk located on the dorsal surface of their flattened heads. Perhaps the common ancestor of cobia and remoras schooled and followed larger fishes, and the population that became remoras adapted to fully realize that niche, while cobia remained schooling as juveniles and occasionally as adults. As Stephen J. Gould states in his paper on the spandrels of St. Mark's cathedral, one is tempted to assign a function to biological phenomenon, while in reality it may not serve a function or may be the byproduct of selection on another trait (Gould and Lewontin, 1979). The trait of schooling in cobia, while probably providing some benefit to the modern fish, may not have risen out of adaptive pressure to school. As of now, it appears that an energetic benefit is not the predominant factor behind the schooling of juvenile cobia, although more studies are needed to add evidence to this.



## ACKNOWLEDGEMENTS

I would like to thank my mentor, Eric McElroy, for all of his assistance and expertise in designing this study and analyzing data. I would also like to thank Mike Denson and the SCDNR staff for help in procurement and care of animals and access to space to perform experiments. Additionally, I would like to thank my fellow honors student Sarah Wiegrefe for taking time out of her busy schedule to help me with coding, and for the honors faculty for providing support and encouragement throughout my undergraduate education.

## REFERENCES

Abrahams, M, Colgan, P. 1985. Risk of predation, hydrodynamic efficiency, and their influence on school structure. *Env Biol of Fishes*. 13(3): 195–202.

Boyd, GL, Parsons, GR. 1998. Swimming Performance and Behavior of Golden Shiner, *Notemigonus crysoleucas*, While Schooling. *Copeia*, 198(2): 467-471.

Davis, MW, Olla, BL. 1992. The role of visual cues in the facilitation of growth in a schooling fish. *Env Biol Fish*. 34:421-424.

Eggers, DM. 1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. *J Fish Res Bd Can*. 33:1964-1971.

Fish, FE. 1995. Kinematics of ducklings swimming in formation: consequences of position. *J Exp Zool*. 273:1-11.

Froese, Rainer and Luna, Susan, eds. 2017. "*Rachycentron canadum*" in FishBase. 2017 version.

Gould, SJ, Lewontin, RC. 1979. The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptionist Programme. Proceedings of the Royal Society of London, Series B, 205(1161):581-598.

Hammond, DL. 2001. Status of the South Carolina fisheries for cobia. Marine Resources Division, South Carolina Department of Natural Resource, Charleston, SC. 22

Hemelrijk CK, Reid DAP, Hildenbrant H, Padding JT. 2014. The increased efficiency of fish swimming in a school. Fish and Fisheries. doi: 10.1111/faf.12072

Herskin J, Steffensen JF. 1998. Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds. J Fish Biol. 53: 366-376.

Ioannou CC, Tosh CR, Neville L, Krause J. 2008. The confusion effect—from neural networks to reduced predation risk. Behav Ecol. 19(1): 126–130.

Killen SS, Marras S, Steffensen JF, McKenzie DJ. 2012. Aerobic capacity influences the spatial position of individuals within fish schools. Proc R Soc Biol Sci Ser B 279:357-364.

Krause J, Godin JGJ. 1995. Predator preference for attacking particular group sizes: consequences for predator hunting success and prey predation risk. *Anim Behav* 50:465-473.

Krause J, Ruxton GD. 2002. P. 47 *In: Living in groups*. Oxford University Press, Oxford

Larkin, PA, Walton, A. 1969. Fish school size and migration. *Ibid.* 26:1372-1374.

Liao JC, Beal DN, Lauder GV, Triantafyllou MS. 2003a. Fish exploiting vortices decrease muscle activity. *Science*. 302:1566-1569.

Marras, S, Killen, SS, Linstrom, J, McKenzie, DJ, Steffensen, JF, Domenici P. 2015. Fish swimming in schools save energy regardless of their spatial position. *Behav Ecol Sociobiol.* 69:219-226.

Milinski, H.; Heller, R. 1978. Influence of a predator on the optimal foraging behavior of sticklebacks. *Nature*. 275: 642–644.

Olson RS, Haley PB, Dyer FC, Adami C. 2015. Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. *Royal Society Open Science*. 2: 150135.

Olson, FCW. 1964. The survival value of fish schooling. *J. Cons. Perm. Int. Explor. Mer.* 29:115-116.

Partridge, B.; Pitcher, T.; Cullen, M.; Wilson, J. 1980. The three-dimensional structure of fish schools. *Behav Ecol and Sociobiol.* 6(4): 277–288.

Pitcher, TJ, Parrish JK. 1993. Functions of shoaling behaviour in teleosts, p. 363-439. *In:* Behavior of teleost fishes. 2d ed. T.J. Pitcher (ed.). Chapman and Hall, London.

Poulin R. 1999. Parasitism and shoal size in juvenile sticklebacks: conflicting selection pressures from different ectoparasites. *Ethology.* 105:959-968.

Turner, G.; Pitcher, T. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. *American Naturalist.* 128 (2): 228–240.

Partridge, B. Johansson; Kalish, J. 1983. The structure of schools of giant bluefin tuna in Cape Cod Bay. *Environmental Biology of Fishes.* 9 (3–4): 253–262.

Pitcher, T.; Magurran, A.; Winfield, I. 1982. Fish in larger shoals find food faster. *Behav. Ecol. and Sociobiology.* 10: 2.

Weihs, D. 1975. Some hydrodynamical aspects of fish schooling, P. 703-718. *In:* Swimming and flying in nature. Vol. 2. T.Wu, C.J. Brokaw, and C. Brennen (eds.). Plenum Press, New York.