

## **Does size matter? Trade-offs in swimming speed and schooling behavior among shiner perch (*Cymatogaster aggregata*) conspecifics of dissimilar size**

Lisandrina Mari<sup>1</sup>, Bill Francois<sup>2</sup>, Chi-Ju Yu<sup>3</sup>

<sup>1</sup>University of Grenoble Alpes, France

<sup>2</sup>Ecole Normale Supérieure, Paris and ESPCI

<sup>3</sup>National Taiwan Ocean University, Taiwan

### **Abstract**

In animals, group motion can be highly organized in oriented and polarized structures. In fish, such movement is referred to as schooling behavior, and while a large body of literature has focused on characterizing this behavior in relation to group size, the implications of having individuals of differences in body sizes on group cohesion and coordination are unexplored. This study focused on this knowledge gap and investigated characteristics pertaining to swimming behavior in surfperch *Cymatogaster aggregata* among pairs of similar and dissimilar size (*i.e.* groups of two big individuals, two small individuals, or one big and one small individual). We analyzed the swimming speed of both individuals, nearest neighbor distance (NND), and characterized the proportion of time spent swimming actively as a group for 9 pairs of fish. Results showed that individuals in big-big groups interact with one another almost half of the time (proportion of time spent swimming together was 48%), a high proportion relative to small-small or big-small groups (12% and 7%, respectively). Swimming speed distributions indicated that the big-big groups were the most active. The average swimming speeds were 135.5 mm/s for big-big groups (equivalent to 1.37 BL/s), 82 mm/s for small-small groups (equivalent to 1.6BL/s), and 116.3 mm/s for groups of dissimilar size (equivalent to 1.05 BL/s for the big fish and 2.32 BL/s for the small fish). Although the observed patterns will require confirmation by completing the analysis with other pairs, and by quantifying other variables linked to locomotion and trajectory, these preliminary results show that while individuals of different size classes tend

to adopt group swimming for shorter time periods than when paired with individuals of a same size class, they are also able to adjust their respective swimming speeds during such periods of interaction to maintain group swimming. The existence of such tradeoffs could explain the capacity of smaller individuals to remain in shoals and schools of mixed size classes.

**Keywords** *Cymatogaster aggregata*, schooling behavior, swimming speed, trajectory analysis, nearest neighbor distance

## Introduction

Movements of animals at the spatial and temporal level are paramount to the completion of many processes (*e.g.* foraging, migration, navigation) and life-history events (*e.g.* dispersal, reproduction). Although the ability to orient and navigate in a specific direction while relying on sensory inputs is commonplace, not all movements are goal-oriented (Benhamou, 2004). Animals may travel randomly while giving no preference to left or right turns, a type of individual trajectory that can be modelled as a random search path (Benhamou & Bovet, 1989). In gregarious species, interaction between members of a group will lead to modifications in individual trajectories (Couzin et al., 2005; Herbert-Read et al., 2012), that will in turn influence group-level cohesion, *i.e.*, the tendency to gather and stay within a short distance from their neighbors, and coordination, *i.e.*, the tendency to adopt the same speed and orientation (Angilletta et al., 2008). Group-level movement can only emerge when individuals reach consensus with neighboring members of the group (Lukeman et al., 2010).

In fish, collective motion is generally organized in highly coordinated structures of polarized individuals (*i.e.*, oriented in a same direction) swimming uniformly and at a short distance from one another, called schools. Schooling has been shown to benefit in spatial exploration, foraging efficiency, awareness of predators, and/or lowering of locomotion energy costs due to hydrodynamic interactions that lead to synchronized swimming patterns among individuals (Krause et al., 2000; Marras et al., 2013; Ashraf et al., 2017). Group advantages are such that

studies report that even individuals swimming at the front of the school may benefit energetic gains compared to swimming alone (Marras et al., 2012) although this is not always the case (Johansen et al., 2010). As such, schooling constitutes a prime example of how interactions between individuals can lead to adjustment of individual trajectories in favor of the group.

Attention has been given to group size (Partridge, 1980; Hoare et al., 2000; Leem et al., 2012), but much less to individual size within a group. Due to the constraining nature of synchronized swimming, schooling fish may usually be assorted by size class because they share the same optimal swimming speed (Hoare et al., 2000, Ward & Krause, 2001). From an evolutionary point of view, associating with conspecifics of a same size can be adaptive, as individuals are less likely to stand out from one another, ensuring protection from predators (Pitcher & Parrish 1993). Exceptions have nonetheless been reported in European minnows (Metcalf & Thomson, 1995), and in guppies (Lachlan et al., 1998), in which large individuals show no preference in joining individuals of the same size class or smaller, the latter being typically considered as weaker competitors. Thus, the relationship between body size and likeliness to join a group might be more complex than initially thought. In nature, mixed size-class and even mixed species associations have been reported (Lachlan et al., 1998; Ward et al., 2002, Smith et al., 2018), but the mechanisms by which individuals of smaller size – and thus, of lower optimal swimming speed – are capable to remain within a group are unclear.

The trajectory of individuals trailing behind a leader hinges on the tradeoff between the capacity to keep up with the leading individual's speed and the anticipation of its trajectory, a compromise largely studied in predator-prey dynamics, where the two individuals differ largely in size (Howland, 1974; Moore et al., 2015, McHenry et al., 2019). Thus, investigating only two fish is interesting because they might exhibit similar anticipatory tactics. Although each individual initially pursues a separated random search path, initiating group swimming will affect the follower – meaning that its path might be correlated to the leader's path – and size difference will drive the adjustment of one individual to the other.

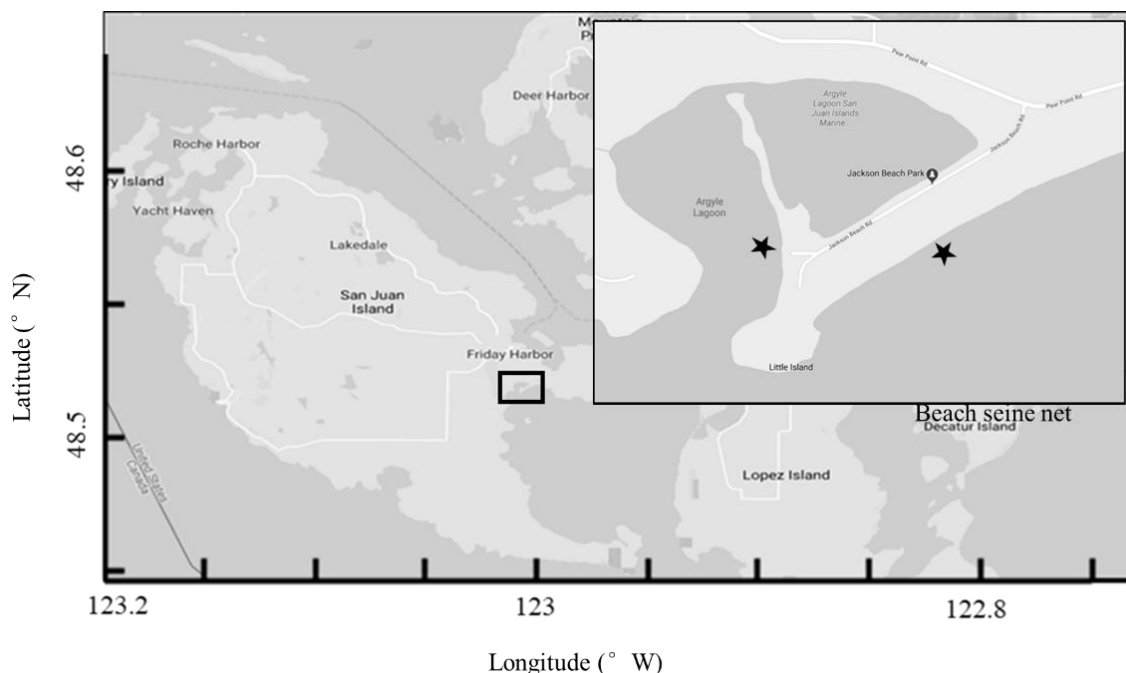
In the present study, we aim at bettering our understanding the effect of size difference on fish swimming trajectory and behavior by investigating locomotion variables (swimming speed, nearest neighbor distance, turning angle) in shiner perch *Cymatogaster aggregata*, a gregarious labriform swimmer, allowed to swim freely in pairs of similar or dissimilar size. We expect same

size conspecifics to maintain high cohesion and coordination, whereas fish of different size classes should adjust several variables pertaining to their locomotion to maintain group swimming. Conforming to the other fish might thus be characterized by observing either i) changes in the speed of one fish or the other, or ii) changes in the trajectory of smaller fish that would, akin to aforementioned predatory strategies, anticipate the other fish's trajectory, especially in turns.

## Materials and Methods

### Fish sampling

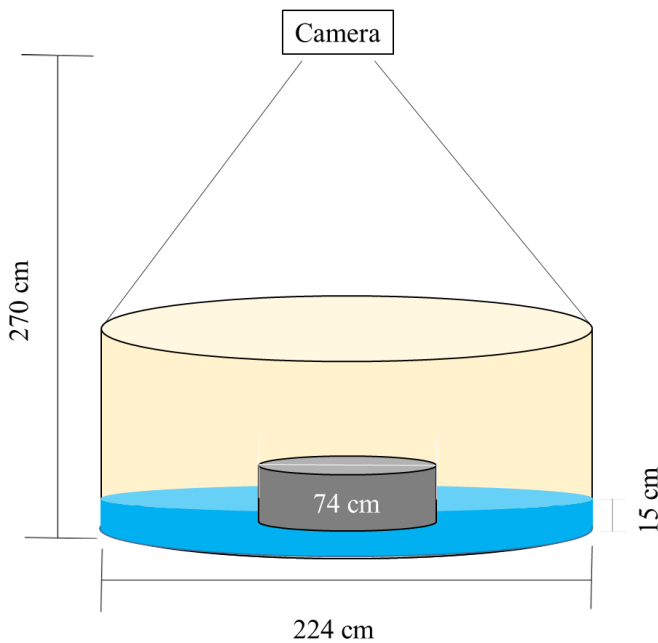
Shiner perch were caught at Jackson Beach and Argyle Lagoon, Friday Harbor, San Juan Island, Washington (48°31' N 123° 0' W, Figure 1) between 24 July 2019 and 14 August 2019 using a beach seine (headline 31.67 m, 48 floats, stretched mesh size 2 cm). Fish were brought back to the laboratory and transferred to holding tanks (1.04 m diameter, water depth 20 cm) immediately. Sea water flow was kept constant in the tanks and water temperature was  $12.935 \pm 0.5$  °C. Fish were exposed to a natural 14:10 light/dark cycle.



**Figure 1.** Study sampling sites of Jackson Beach and Argyle Lagoon, Friday Harbor, San Juan Island, Washington (48°31' N 123° 0' W, Figure 1) between 24 July 2019 and 14 August 2019 using a beach seine (headline 31.67 m, 48 floats, stretched mesh size 2 cm). Fish were brought back to the laboratory and transferred to holding tanks (1.04 m diameter, water depth 20 cm) immediately. Sea water flow was kept constant in the tanks and water temperature was  $12.935 \pm 0.5$  °C. Fish were exposed to a natural 14:10 light/dark cycle.

## Experimental set-up

Individuals were measured for total length (TL, mm) from snout to tip of the tail. Fish were arranged by size-class, with fish of TL < 70 mm considered as ‘small’, and of TL > 90 mm considered as ‘big’. TL ranged from 42 to 72 mm (mean of  $55 \pm 6.76$  mm, SD) for small individuals, and from 86 to 135 mm (mean of  $104 \pm 10.46$  mm) for big individuals (Table 1).



**Figure 2.** Schematic diagram of the experimental set-up.

For the schooling behavior experiment, fish were grouped as pairs according to the size ratio of the two individuals, calculated as:  $\text{Size ratio} = L_B / L_S$ , with  $L_B$ : total length of bigger fish,  $L_S$ : total length of smaller fish. Three types of pairs were constituted: two types of same-size pairs, with a size ratio of  $1.1 \pm 0.05$ : small-small (S-S), big-big (B-B); and one type of dissimilar-size pairs: big-small (B-S), with a ratio of  $2.0 \pm 0.15$ . Each pair was kept in isolated tanks and starved for a minimum of 9 hours prior to the experiment.

The experimental tank was constituted of a round tank of 2.24 m diameter and a smaller island shaped tank (0.74 m diameter) placed in the center to create a circular water channel, with a water depth of 15 cm (Figure 2). The experimental tank was shielded from outside stimuli by a tent, and water flow was kept constant but low so as not to affect swimming behavior during the trials. Each pair was introduced into the experimental tank simultaneously, left to acclimate in the experimental tank for one hour, and left to swim spontaneously for two hours. Movement and behavior were then recorded for a subsequent three hours with a wide angle camera (GoPro Hero 4) mounted 2.7 m above the tank with a 2.7 k resolution, linear field, at 30 frames per second. Trials were conducted on 20 pairs of each type once, accounting for a total of 60 pairs.

**Table 1.** Total length (TL, mm) and size ratio for each pair of fish used in the experiment.

<b>Group No.</b>	<b>TL1</b>	<b>TL2</b>	<b>Ratio</b>	<b>Group No.</b>	<b>TL1</b>	<b>TL2</b>	<b>Ratio</b>
1	42	49	1.17	31	58	106	1.83
2	45	45	1.00	32	59	62	1.05
3	45	95	2.11	33	60	60	1.00
4	46	53	1.15	34	60	65	1.08
5	46	90	1.96	35	60	106	1.77
6	46	97	2.11	36	60	120	2.00
7	46	100	2.17	37	62	64	1.03
8	46	105	2.28	38	62	70	1.13
9	48	95	1.98	39	63	115	1.83
10	49	52	1.06	40	69	70	1.01
11	50	53	1.06	41	72	131	1.82
12	50	59	1.18	42	86	86	1.00
13	50	95	1.90	43	90	95	1.06
14	51	60	1.18	44	92	94	1.02
15	52	94	1.81	45	95	96	1.01
16	53	54	1.02	46	95	97	1.02
17	53	57	1.08	47	96	97	1.01
18	53	109	2.06	48	96	97	1.01
19	53	120	2.26	49	96	100	1.04
20	54	57	1.06	50	97	102	1.05
21	54	110	2.04	51	97	105	1.08
22	55	57	1.04	52	99	100	1.01
23	55	97	1.76	53	100	105	1.05
24	55	110	2.00	54	101	106	1.05
25	55	110	2.00	55	101	110	1.09
26	56	60	1.07	56	106	108	1.02
27	56	104	1.86	57	107	110	1.03
28	56	105	1.88	58	115	122	1.06
29	57	60	1.05	59	117	122	1.04
30	58	60	1.03	60	127	135	1.06

### **Video analysis**

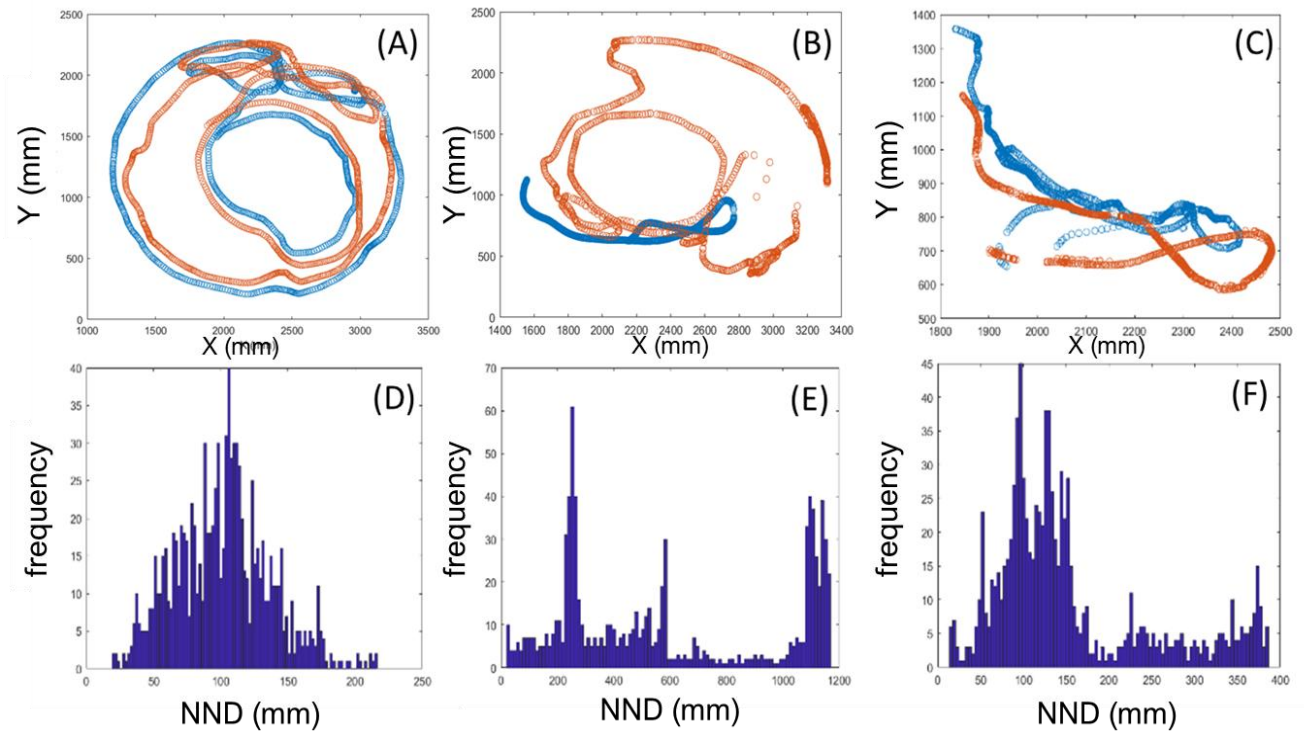
Videos were converted into image sequences using Video to JPG Converter software (<https://www.dvdvideosoft.com/products/dvd/Free-Video-to-JPG-Converter.htm>) and processed with MATLAB R2018a (MathWorks) to adjust contrasts. Because all the pairs of the study were moderately active, images were extracted and tracked at a rate of 10 frames per second, which was adequate to estimate all relevant parameters for the analysis. Each individual fish movement was tracked for 1 minute every 10 minutes, and coordinates and traces of trajectories were

extracted using FastTrack v4.8.3 (<http://www.fasttrack.sh>). Swimming speed, nearest-neighbor distance (NND) between two fish (calculated as the Euclidean distance between the pair's coordinates at a given time), and turning angles were computed using MATLAB. The cutoff threshold at which fish were considered to interact together was estimated by analyzing the distribution of NNDs, and assessed to be at around 3 body lengths (BL). The cutoff threshold at which fish were considered to be actively swimming was estimated by analyzing the distribution of swimming speeds, and assessed to be around 0.5 BL/s.

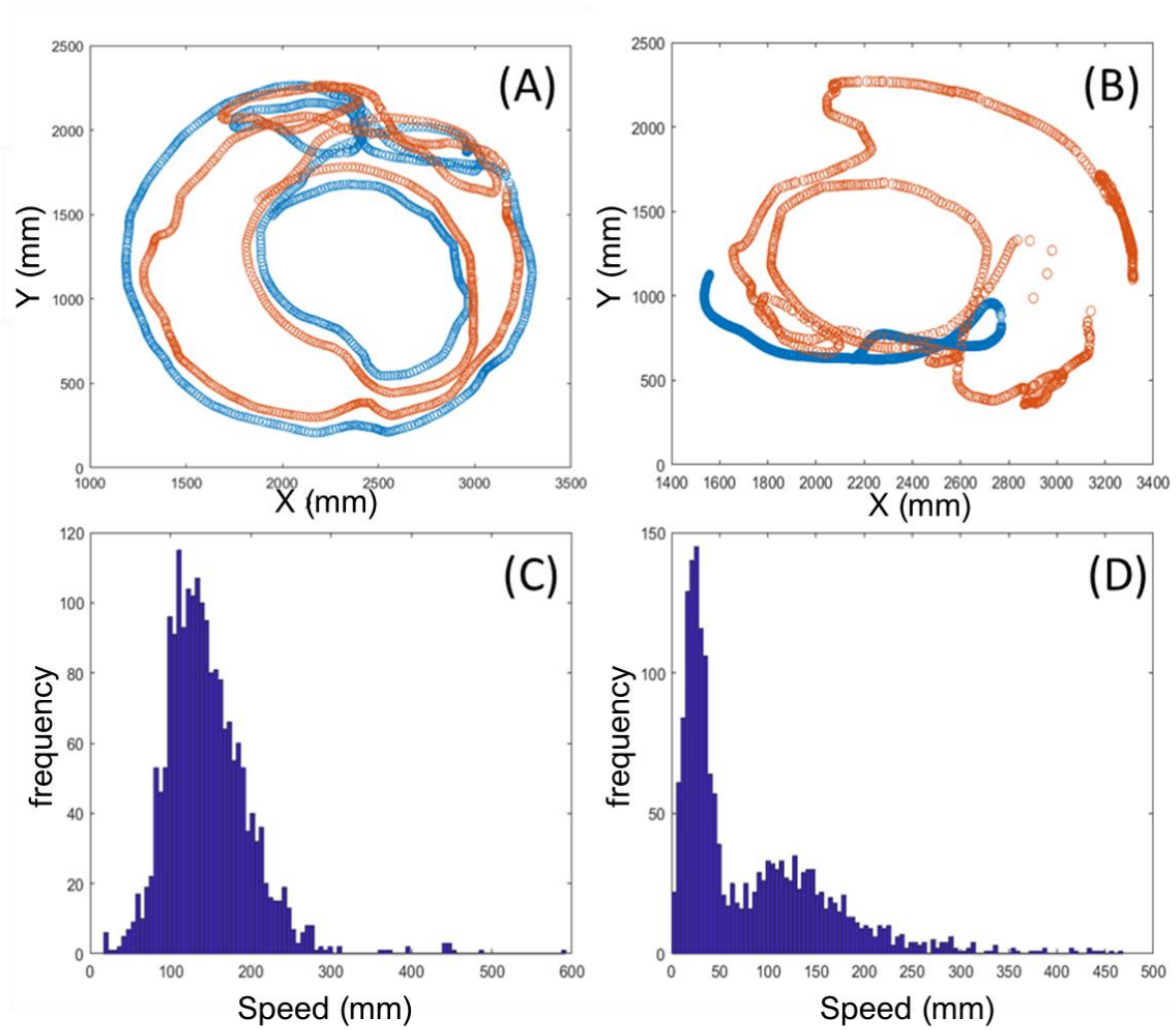
## Results

The distribution of NND was gaussian-centered in pairs exhibiting group swimming (Figures 3A & 3D), and non-normal in pairs not interacting for most part of the recording (Figures 3B & 3E). In most cases, we observed a sum of the two distributions (Figures 3C & 3F), indicating fish interacted only part of the time. This bimodal distribution allowed us to derive the NND threshold at which fish are considered to be interacting. Similarly, the distribution of swimming speed was gaussian centered actively swimming pairs (Figures 4A & 4C), and non-normal in pairs where some fish were not swimming during part of the recording (Figures 4B & 4D). The bimodal distribution of pairs exhibiting part-time group swimming was constituted of two Gaussians, one showing noise measurements on non-moving fish, due to tracking uncertainty of the center of mass, and the other one showing the swimming speed distribution. The visible cutoff between these two curves allowed us to derive the speed threshold at which a fish can be considered to be swimming.

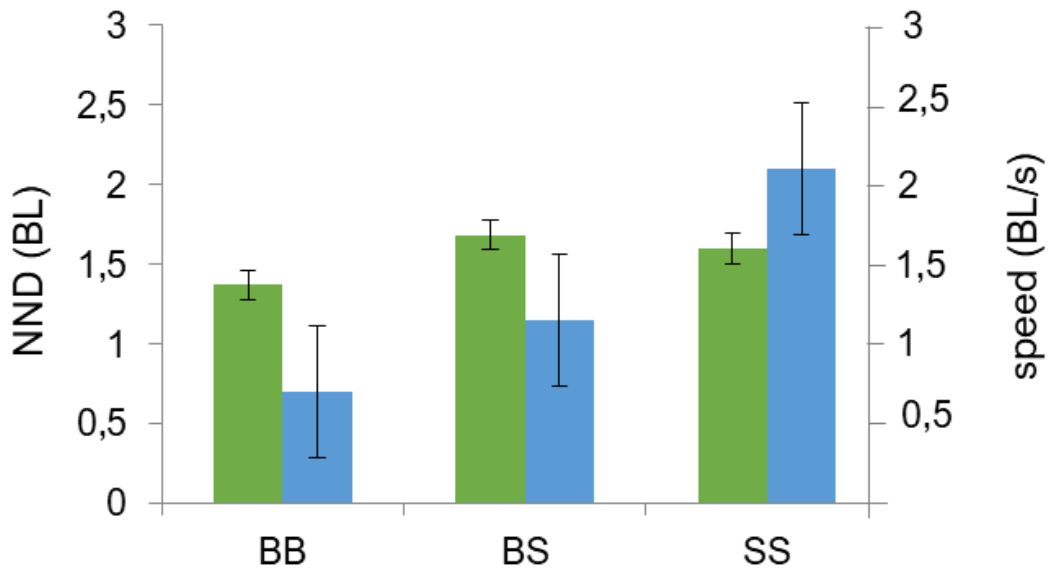
By applying these two thresholds, the amount of time fish spent swimming together was 48% for the big-big pair, 7% for a big-small pair and 12% for a small-small pair. The average NND was 0.7 BL for big-big, 0.7 to 1.6 BL for big-small, and 2.1 BL for small-small (Figure 5). The average swimming speeds were of 135.5 mm/s (1.37 BL/s) for big-big, 116.3 mm/s (1.05 BL/s for the big fish and 2.32 BL/s for the small fish assuming they go at the same speed), and 82 mm/s (1.6BL/s) for small-small.



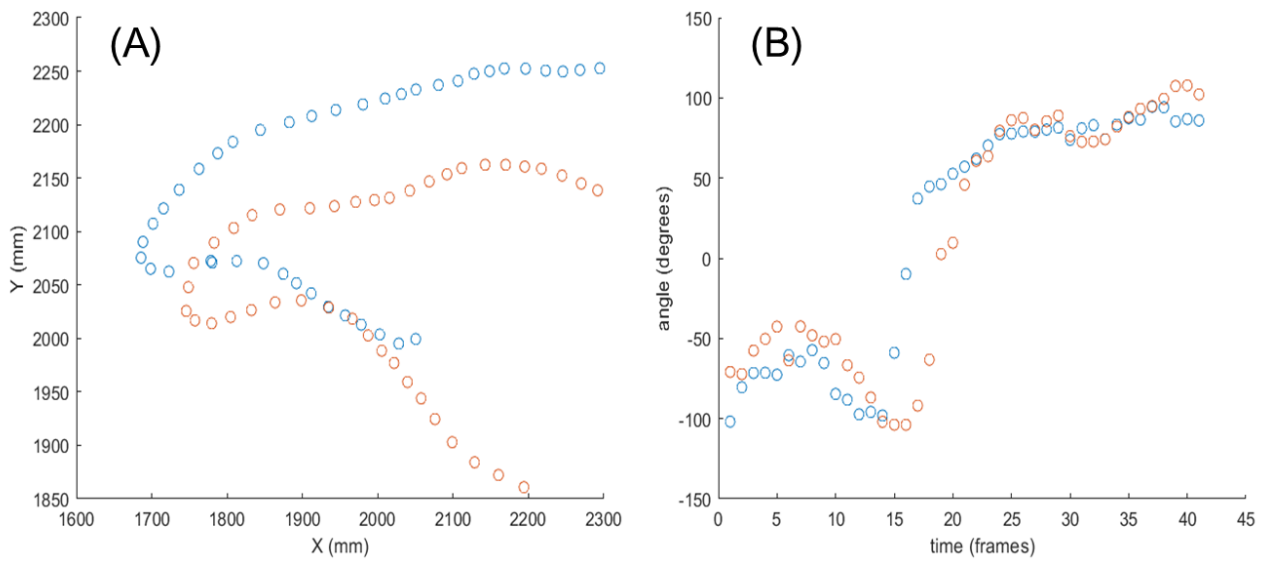
**Figure 3.** Trajectories over 1000 frames of a (A) big-big pair exhibiting group swimming, (B) small-small pair not exhibiting group swimming, (C) small-small pair exhibiting group swimming part of the time. Colors indicate different individuals. Frequency distribution of NND over 1000 frames for (D) big-big pair exhibiting group swimming all the time, (E) non group swimming small-small pair, (F) Small-small pair exhibiting group swimming part of the time.



**Figure 4.** Trajectories over 1000 frames of a (A) big-big pair exhibiting group swimming and (B) small-small pair exhibiting group swimming part of the time. Colors indicate distinction between individuals. Frequency distribution of swimming speed over 1000 frames for (C) big-big pair swimming all the time, (D) small-small pair swimming only part of the time.



**Figure 5.** Average NND (blue) and speed (green) for pairs of each type, normalized by fish body length.  $N = 2$  per pair type, means are presented  $\pm$  SD.



**Figure 6.** An example of trajectory angle during a turn for a pair of big fish (blue) and small fish (red) where the big fish initiates the turn, with (A) coordinates, and (B) turning angle in degrees measured between a given frame and the next one over time.

## Discussion

In this study, we investigated swimming behavior and trajectory among pairs of fish of similar and dissimilar size, focusing on group cohesion and coordination. Nearest neighbor distance measurements and qualitative observation of trajectories revealed that individuals of similar size tended to adopt group swimming more frequently, whereas heterogenous pairs preserved their individuality most of the time. However, when dissimilar-size fish started exhibiting group swimming, both fish adjusted their swimming speed (decreasing speed for the bigger individual, and increasing speed for the smaller one) which indicates they are capable to find a compromise, although only over a short period of time.

On average, the big-small pairs spent 7% of the time swimming together. Considering this small proportion of time, it is possible that fish of different sizes may have intentionally avoided each other. While bigger fish can be perceived as advantaged competitors by smaller ones (Hoare et al., 2000), we assume the benefits of group swimming might outweigh the perception of the other fish as a competitor, especially in the lack of resource to compete for in a trial. Furthermore, each pair was isolated prior to the trial, so that the two fish would be familiar with each other before introduction in the experimental tank. As such, avoidance could be linked to swimming ability limitation for the smaller fish.

However, it is certain that our observations present only a small fraction of the ensemble of trajectories fish have taken during the whole duration of the trial, and present a clear bias in that sense. Due to time constraints, we presented in this paper results for only 9 pairs (3 for each pair type), using 10 minutes video recordings. Trials lasted for two hours in total and proper analysis of the available footage of all the trials that were carried out is required to better identify trends among pairs.

In the near future, completing the current study using a longer timescale will need to be coupled with quantifying more variables linked to locomotion and trajectory. When investigating trajectories under random search path models, the estimation of the path tortuosity is an important criterion that efficiently informs of the spatial use (Benhamou 2004, Nams 2006, Angilletta et al., 2008). It will be relevant to analyze whether smaller fish use less tortuous paths than bigger ones, indicating that they attempt to anticipate the bigger fish's trajectory in order to

keep up with larger and faster swimming leaders. A joint analysis of tortuosity with swimming speed and turning angles calculations would allow the identification of conforming behavior (Figure 6). Finally, the use of schooling variables such as relative position in the group (leader or follower) through time and polarization would inform us of the coordination capacity of conspecifics of different sizes.

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