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Collective responses of a large mackerel school depend on the size and speed of a robotic fish but not on tail motion

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Abstract

Robotic animal models provide an increasingly popular method for animal behaviour research. Yet, actuated fish models have been mostly used to study animal interactions in small-scale controlled experiments. This study, conducted in a semi-controlled setting, investigates robot interactions with a large wild-caught marine fish school (~ 3 000 individuals) in their natural social environment. Two towed fish robots were used to decouple size, tail motion and speed in a series of sea cage experiments. Using high resolution imaging sonar, we monitored and classified the school's collective reaction towards the fish robots as attraction or avoidance. In contrast to previous studies, we found fish reactions to the tail motion to be insignificant. We interpret this result as evidence that fish schools rely on different sensory cues in noisy natural environments. We also found that two key releasers – the size and the speed of the robotic fish – were responsible for triggering either evasive reactions or following responses. The fish evaded a fast moving robot even if it was small. However, mackerels following propensity was greater towards a slow small robot. When moving slowly, the larger robot triggered significantly more avoidance responses than a small robot. Our results suggest that the collective responses of a large school exposed to a robotic fish could be manipulated by tuning two principal releasers – size and speed. These results can help to design experimental methods for *in situ* observations of wild fish schools or to develop underwater robots for guiding and interacting with free-ranging aggregated aquatic organisms.

1. Introduction

Using robotic models in animal behaviour research advances our understanding of social interactions and can provide guidance for manipulation of animal behaviour. Yet, a main challenge remains to ascertain how these techniques can be applied to wild animal aggregations in their natural social settings. Here, we present the first experimental attempt to explore collective responses of a natural-sized marine fish school using robotic models in a semi-controlled aquatic environment.

Animal models allow for the simulation, decoupling and manipulation of sensorial cues and behavioural patterns in a controlled manner during animal behaviour experiments. Over the years, various artificial renditions have been utilized

such as static dummies [1, 2], pictures and mirrors [3], audio [4] and video [5, 6] playbacks, computer animations [7-10] and robotic models [11, 12] in different taxa. These different approaches permit decoupling of actuation from other parameters and allow for independent manipulation of the various sensory cues.

The use of robots in the study of animal behaviour in general, and of collective behaviour in particular, is getting increasingly more attention [12, 13]. In this context, Krause *et al.* [12] defined a robot as a “machine that is able to physically interact with its environment and perform some sequence of behaviours, either autonomously or by remote control”. This approach allows a higher degree of standardization of the dynamic patterns and realism based on the morphological appearance and behaviour presented during staged social interactions [12] as opposed to the other renditions. Importantly, as robots mimic the physical presence of conspecifics or heterospecifics, this technique provides an efficient means to explore dynamic interactions that rely on multimodal sensory systems, an approach not feasible with other virtual model approaches often limited to the visual field only.

Robotic animal models have been used in several studies on collective behaviour of aggregated fish. Ward *et al.* [14] used fish models to show that it took two or more (robotic) conspecific fish to lead the fish school around a predator replica. Faria *et al.* [13] used a fish dummy manipulated by an external robotic arm to validate models of collective behaviour. Polverino *et al.* [15] found that fish were attracted to their robotic counterpart but to a lesser degree as to the real members of the school. They also found that fish tail undulations increase the degree of their attractiveness. In another tank study, Marras and Porfiri [16] investigated the interaction of a robotic fish with golden shiners (*Notemigonus crysoleucas*) and found that fish preferred to spend time in the vicinity of the robotic fish when the robot's tail was beating. Their following work investigated the interaction between zebrafish (*Danio rerio*) and robots, and revealed that the number of robots present in the tank affected the zebrafish' reactions [15]. Zebrafish also modified their behavioural responses when observing a robot with a moving tail [17]. Swain *et al.* [18] used a predator model controlled by visual feedback from a school of golden shiners to change the school's behaviour .

Tinbergen's hypothesis of releasers, i.e. external sensory stimuli necessary to trigger an individual's behavioural response, states that the innate behaviour is never a reaction to the environmental situation as the whole but to only a few parts of it [19]. From an engineering point of view, Tinbergen's hypothesis also offers a possibly very appealing robot minimal design paradigm, which is widely recognized when designing robots for interaction with humans [20]. It suggests that for efficient manipulation and interaction with animals, simplified robotic models, being only superficially similar but presenting the key releasers, would be sufficient. An important objective then becomes to identify and implement those key features in robotic models.

There are several key features that cause behavioural responses in fish. Schooling fish behaviourally act on the combined inputs from diverse sensory pathways such as vision [21], chemical-sensing [22, 23], acoustic or hydraulic cues sensed by the lateral line system [24, 25] or inner ear [26, 27]. The sensory signals originate both from social and predator interactions. In particular, when in schools,

fish can learn about an immediate danger directly by gathering sensory information during a predator's approach or indirectly from the escape behaviour of risk-aware schooling partners [23, 28-31]. The importance of the biomimetic locomotion of the tail is explained by sensitive lateral line organ that can sense the undulating motions created by other fish (or robots) [32]. It is also well established that size and speed are used as proxies for determining whether an individual fish is perceived as a conspecific or as a potential threat [33-36]. For example, banded killifish (*Fundulus diaphanus*), given a shoal choice, preferred to join a shoal constituted of same-size fish, an effect amplified by an increasing predation risk [37]. In their natural marine environments, solitary and aggregated fish prey generally encounter a variety of predators that differ in size, swimming performance or hunting strategies [38]. It is assumed that fish prey fine-tune their anti-predator reactions to the nature of the potential threats to enhance their likelihood to survive an attack. Predators' size and velocity were found to affect the distance at which zebra danios (*Brachydanio rerio*) initiate an evasive reaction [36], with larger and faster predators inducing greater escape responses. The field of biomechanics has provided valuable information regarding the dynamics of predator-prey interactions in aquatic organisms [38-41], particularly by highlighting a positive relationship between the swimming speed and body length of fish and top cetacean predators [39, 40] and its ultimate effects on the outcome of attack-escape sequences. Therefore, it is reasonable to assume that tail beat motion, size and speed of the robotic model can be considered key features that may alter the behaviour of the fish.

The fish-robot interaction studies have so far been conducted in laboratory conditions, usually in small tanks, involving a limited number of fish. In controlled laboratory environments, the signal to noise level for the different sensory signals can be controlled and kept high, and each of the sensorial pathways can be independently tested. However, under more noisy natural conditions, the signal to noise level for these sensory pathways is lower, making it unclear how the laboratory results can be generalized to large fish schools in their natural habitat [42]. The next challenges are, therefore, to establish how robotic fish interactions may be affected by a decrease in signal to noise ratio for the different sensory pathways and by the size of the focal schools.

The objective of this paper is to test how fish react to different key features of a robotic fish model in a semi-natural environment, as a step between the laboratory experiments and an open ocean situation. We introduced robotic models to schooling Atlantic mackerels (*Scomber scombrus* Linnaeus, 1758) in a net pen, where the social and physical environments in terms of water current, sound levels and social conditions (large school) are more similar to the natural situation. We hypothesized that schooling mackerels would be *i*) more strongly attracted towards the robot if the tail is beating with a similar frequency as the fish in the pen, that the robot's *ii*) size and *iii*) swimming speed would be important in terms of how the robot is able to blend in or cause behavioural avoidance reactions of schooling mackerels.

2. Materials and methods

2. 1. Mackerel school and housing facilities

To test our hypotheses, we investigated the collective responses of a large wild-caught school of adult mackerels towards fish robots that differed in their sensory signature and swimming activity. Our goal was to test whether the size, speed and the swimming pattern of the robotic models affect the collective response of mackerels. Mackerel are pelagic fish that form extremely cohesive and highly responsive schools capable of displaying coordinated manoeuvres in response to environmental perturbations or when under a predator's attack. *S. scombrus* is a voracious fish species and important consumer of zooplankton [43] forming schools that can reach sizes up to several millions of individuals generally organised in size-classes [44]. In the Northeast Atlantic, mackerels are commonly preyed upon by large marine mammals such as killer whales (*Orcinus orca*) [45].

The experiments described in this article were conducted between September 2 and September 3 2014 at the Institute of Marine Research aquaculture facility at Austevoll, Norway (60°5'20 N 05°15'58 E). Prior to the experiment, wild mackerels were lured into an open aquaculture rectangular net pen (sea cage: 12.5 m long x 12.5 m wide x 13.5 m deep; figure 1) at night using fish fodder, and the cage was closed by pulling up the net in the morning followed by a transfer into a holding pen. The catching and transfer was done by gently pulling-up the net to avoid physical impairments (e.g. scale loss and skin injuries). The process was repeated over a period of several days. The fish were held in the net pen for approximately 2 months prior to the experiments to allow them to acclimate to their captive conditions. Mackerels were fed with standard small-sized aquaculture pellets in addition to any naturally available prey that flowed into the net pen. The fish remained in the net pen during the complete duration of the experiment. Fish total length and weight were measured before the experimental period, $n = 19$; body length = 41.05 ± 2.82 cm; weight = 715.37 ± 148.3 g; all results are expressed as a mean $\pm$ SD (standard deviation).

All experimental tests were conducted directly in the net pen (figure 1). A calibrated upward-looking 120 kHz split-beam echosounder with a 7 degree beamwidth (Simrad EK 60, Kongsberg Maritime AS, Horten, Norway) mounted on a gimbal was deployed close to the bottom of the experimental net pen. The echosounder was used to continuously monitor the fish vertical distribution in the water column and to estimate the number of fish in the pen using echo integration [46]. The data collected were imported in Echoview 5.2 (SonarData Pty. Ltd., Tasmania, Australia) to estimate the school's density. The total number of fish inside the pen just prior to the experiment was estimated by integrating the backscattered echo energy (Nautical area scattering coefficient, NASC [47]) over the vertical fish distribution ($NASC = 18163 \text{ m}^2 \text{ n.mi}^2$). By assuming a uniform horizontal distribution across the 12 m x 12 m pen ($A = 144 \text{ m}^2$) and a target strength for 200kHz of $TS = 20 \log_{10}(41) - 80 \text{ dB re } 1 \text{ m}^2$ (Egil Ona, pers. comm.), which gives a $\sigma_{bs} = 2.11 \cdot 10^{-11} \text{ m}^2$, the number of fish inside the pen was estimated to $N = NASC \cdot A \cdot (\sigma_{bs} 1852^2 4\pi)^{-1} \approx 3000$ individuals and a biomass of approximately 2 metric tonnes.

A horizontally-looking high-resolution imaging sonar, ARIS (Adaptive Resolution Imaging Sonar, Sound Metrics Corporation, Bellevue, WA, USA), operating at 3 MHz, was mounted on one side of the net pen at a 1 m depth. The ARIS was used to observe the school collective reactions towards the fish robots. The sonar imaging recordings were imported into ArisFish software (Sound Metrics Corporation, Bellevue, WA, USA) to analyze fish reactions.

2.2. Robotic fish

Two robotic fish were used as animal models (figure 2). The two robots differed in size and were towed through the fish school at different speeds either passively or by actuating their tail. Robots were scaled to imitate the shape of live mackerel. One of the robots matched the size of an average adult mackerel whereas the other was scaled up while maintaining the same proportions. The smaller robot was 34 cm long and weighted 631 g. The larger fish robot was 54.5 cm long and weighted 1582 g. A computer-aided design model of the mackerel was created from a photo and scaled. The smaller size robot was chosen based on typical mackerel sizes from commercial catches in the area. Both models were built having a 3D-printed rigid head housing the electronics and actuator, and a soft, silicone tail, casted with the help of a 3D printed mold. An acrylic glass caudal fin was attached to the tail. A servo motor with an infrared remote control was used to adjust the amplitude and frequency of the tail beat.

Tail beat frequency was measured following a straightforward procedure: 35 individuals were randomly selected when swimming in a stationary situation in the housing net pen. Each fish was manually tracked and we counted the number of tail beats during a variable time slot, which depended on the amount of time the fish was visible along its path. The tail beat frequency of actively swimming mackerels was 1.93 ± 0.52 tail beats per second (mean $\pm$ SD).

During our tail beat experiment the tail beat was roughly matched with the measured tail beat of mackerel 1.93 ± 0.52 (mean $\pm$ SD) and a slightly lower frequency of 1.8 tail beats per second was used for the robot. The amplitude of the tail beat is expressed by the lateral movement of the caudal fin from one side to another. Approximate amplitude of the tail was calculated for the both robots using results from Bainbridge [48] and adjusted by trial and error in water. Amplitude of 8 cm was used for the smaller and 12 cm for the bigger model.

The robotic fish were pulled transversally across the net pen at 1 m depth by attaching fishing line to the model and leading it through a block at the arriving end of the pen (figure 1). The fishing line was connected to an electric engine placed at the net pen opposite side allowing to control precisely the towing speed. The speeds were recorded by timing the tow duration and were consistent between trials. A total of 6 random experiments were used to determine the robot's speed. Pulling speed of 0.75 ± 0.01 meters per second for slow and speed of 1.66 ± 0.03 meters per second for fast experiment was used (mean $\pm$ SEM, standard error of mean). During each experiment, a control treatment that consisted of the fishing line without a model was used to test whether the noise from the releasing gear, activity on the dock, and the motion of the fishing line itself may have caused the fish reactions.

2.3. Sonar measurements and video processing

Using a high-resolution imaging sonar, we observed mackerel's 2 distinct collective reactions towards the robots: the fountain effect and a collective attraction towards the robotic animals. The fountain effect is a commonly used escape manoeuvre exhibited by schooling fish when under a predator's attack during which the school first splits into two groups on each side of the path of the threat and after regroups behind it [49] (figure 3). An attraction response is defined as the dynamic swimming of fish in the direction of the robot model.

The fountain effect and collective attraction were both evaluated determining the strength of the reaction – unnoticeable, weak or strong. The strong reaction was defined as the uniform response of the whole fish school, whereas the weak one was defined as the noticeable reaction in close proximity of the robot without triggering any change of the swimming pattern for the fish further away. During the weak response the imaginary border of the fish school stayed intact, contrary to the strong reaction which induced the temporary transformation of the shape of the fish school. Unnoticeable response was defined as individual avoidance of the robot without any signs of collective movement.

2.4. Procedure

Experiment 1

We tested the collective reactions of schooling mackerels towards two robotic fish that differed in size and biomimetic locomotion. We employed a randomized-block design where the presentation order of the different stimuli was randomized. The schooling fish were exposed to each combination of stimuli (size x tail-beat frequency + control) one time (5 exposures) and then were exposed to a reverse order sequence of stimuli in order to counterbalance order effects (5 exposures; for a total of 10 exposures). Two consecutive robotic fish exposures were separated by at least 15 minutes to allow the fish to return to a similar schooling dynamic as prior to exposure (verified using real-time acoustic observations). As mackerels generally swam actively all over the sea cage, a limited quantity of food pellets was released using an aquaculture automatic feeder close to the surface 2 minutes before the release of the robotic fish to make sure that the fish encountered the robotic fish. The period of time before the release of the robot and the small quantity of food offered insured that all the food items were ingested while mackerels stayed close to the surface.

Experiment 2

In this experiment, we tested the collective reactions of schooling mackerels towards two robotic fish that differed in size and swimming speed. We employed a randomized-block design where the presentation order of the different stimuli was randomized. We conducted 4 consecutive blocks where two consecutive blocks were separated by at least 20 minutes. During a block, schooling fish were exposed to each combination of stimuli (size x speed) one time (4 exposures) and then were exposed

to a reverse order sequence of stimuli in order to counterbalance order effects (4 exposures; for a total of 8 exposures per block). Within a block, two consecutive exposures were separated by at least 10 minutes to allow the fish to return to a similar schooling dynamic as prior to exposure. An observer (GR) verified that the fish returned to similar schooling dynamic as prior to exposure using real-time acoustic videos. Again before each test, mackerels were lured close to the surface by throwing a small quantity of food pellets using the automatized feeder 2 minutes before the release of the robot fish. A total of 32 exposures were conducted during this experiment.

2.5. Statistical analysis

We used generalized linear models (GLZs) with binomial distribution and probit link function to examine the effects of the experimental treatments (Experiment 1: robot size and tail-beat frequency; Experiment 2: robot size and speed) on the collective reactions (probability of avoidance responses and following behaviour) of schooling mackerels. For both experiments, we included the interactions between the two experimental treatments in the models. For each GLZ, we reported the Wald χ^2 statistic and p value. All statistical tests were performed in Statistica 11 (StatSoft Inc.; www.statsoft.com).

Our main objective was to explore the effect of the multi-sensory signature of different robotic fish on the collective response of a mackerel school which size matched the social conditions in the open ocean. Due to logistical restrictions, we were unable to create smaller subsets to control for pseudoreplication [50], as is common practice in smaller scale experiments. However, the large number of fish present in the sea cage and their highly dynamic swimming pattern have created a substantial mixing of individuals ensuring that not always the same fish directly encountered the different robotic fish during each test. In addition, the randomized-block experimental design employed in both experiments where the presentation order of the different stimuli was randomized and the interval of time between consecutive exposures may have prevented habituation and a sequence effect in responsiveness as suggested by Schleidt *et al.* [51]. For both experiments, we did not include the control data (fishing line alone) in the GLZs as the control condition never triggered a reaction from the fish school.

3. Results

3.1. Experiment 1: Fish robot biomimetic locomotion

We did not find a significant main effect of the size of the robots (GLZ, Wald $\chi^2_1 = 0.63$, $p = 0.43$) or their tail-beat frequency (GLZ, Wald $\chi^2_1 = 0.54$, $p = 0.46$) on the probability of a collective avoidance reaction of the schooling mackerels (figure 4). The interaction between the robot size and tail-beat frequency was also not statistically significant (GLZ, Wald $\chi^2_1 = 1.09$, $p = 0.29$).

Tail-beat frequency did not influence mackerels propensity to follow the robots (GLZ, Wald $\chi^2_1 < 0.001$, $p = 1$) (figure 5). However, even though it failed to

reach the conventional level of statistical significance (GLZ, Wald $\chi^2_1 = 3.45$, $p = 0.06$), we observed a pattern towards a higher propensity of mackerels to follow the larger fish robot than the smaller, this independently of the robots' tail-beat frequency (figure 5a). The interaction between size and tail-beat was not statistically significant (GLZ, Wald $\chi^2_1 < 0.001$, $p = 1$).

3.2. Experiment 2: Fish robots' size versus swimming speed

Both the size (GLZ, Wald $\chi^2_1 = 4.47$, $p = 0.03$) and the speed (GLZ, Wald $\chi^2_1 = 4.86$, $p = 0.03$) of the robot significantly affected the probability of a collective avoidance reaction exhibited by the schooling mackerels. The interaction between the size and speed of the robot was not statistically significant (GLZ, Wald $\chi^2_1 < 0.001$, $p = 0.99$). The larger fish robot induced significantly more avoidance reactions than the smaller one (figure 6a). In addition, a speedy robot fish was more effective at eliciting an avoidance reaction than a slow model (Figure 6b).

We found a significant effect of the size of the fish robot (GLZ, Wald $\chi^2_1 = 11.30$, $p < 0.001$) and the speed at which it crossed the school (GLZ, Wald $\chi^2_1 = 12.35$, $p < 0.001$) on the probability of a mackerels' following reaction towards the robot. Regarding the robot's size, mackerels followed more the small robot than the larger one (Figure 7a). Schooling mackerels followed more a slow swimming fish robot than a speedy one (Figure 7b). The absence of a significant interaction between the size and speed of the robot (GLZ, Wald $\chi^2_1 < 0.001$, $p = 0.99$) suggested that for both the large and small fish robot, an increasing speed decreased the propensity of mackerels to follow the fish robot.

4. Discussion

We present the first experimental attempt to explore collective responses of a natural-sized marine fish school using robotic models in a semi-controlled environment; providing a social context (~3 000 individuals) that is lacking in previous experiments. By testing a wild-caught mackerel school in social conditions similar to what these fish naturally experience, our study brings new insights on the efficiency of the robotic model approach to investigate how large fish shoals react in unison in response to environmental perturbations or predators. Moreover, our study also provides practical information for the further development of animal-like robots to study massive aggregations of wild animals *in situ*.

Our results revealed that the tail motion of the fish robots did not influence mackerels' avoidance responses, whereas size and speed of the fish robots strongly affected mackerel's reactions. Both fast and slow moving robots induced strong evasive responses. Therefore, our results show that the size of the robots and the speed at which they crossed the school are key factors triggering fish collective predator avoidance behaviour.

The biomimetic locomotion of the robotic fish did not act as a releaser of the mackerels following behaviour towards the model, in contrast to the findings of

previous studies conducted on zebrafish [15] and golden shiners [16] in controlled laboratory conditions. In both these studies, the biomimetic locomotion was found to be the key feature determining the fish responses. If the ecology of the focal species and the artificial social conditions in which fish have been tested can explain a part of this discrepancy, our study highlights that fish in controlled laboratory conditions may act on different sensory cues compared to noisy natural conditions and/or when swimming in large shoals. Consequently, care must be taken when extrapolating the results obtained with sole or few individuals to the collective behaviour of large schools in natural environments.

In a sea cage experiment on a large Atlantic herring school (*Clupea harengus*), approximately 60 000 individuals, Rieucou *et al.* [52] reported that herring collective escape reactions depend on the sensory signature of different dynamic predator models to which fish were exposed to. Herring responded to the combination of visual and hydrodynamic cues produced by the swimming pattern of the predator-shaped models. Models presenting the highest colour contrast against the visual background and producing the maximum drag induced the strongest collective evasive reactions. Similar to this study, our mackerels only reacted to some conspicuous features of the robots. If some fish species reacted to subtle sensory characteristics of animal models (e.g. robot tail-beat frequency) during experiments in controlled experimental settings, in a naturally noisy environment with a different signal to noise ratio acting upon more perceivable cues may minimize the costs of making erroneous anti-predator or foraging decisions. It is therefore reasonable to assume that the ability of mackerels to detect changes in the biomimetic locomotion of fish robots could have been impaired by the highly dynamic physical environment. The development of an experimental framework aiming at understanding how environmental noise constrains the mechanisms at work during collective reactions of schooling fish is needed.

This study provides another example of robot-animal interaction in a growing body of studies where robots are used as tools in experimental biology. In our case, the robotic dummies allowed us to test the effect of biomimetic locomotion to fish reaction that, contrary to expectations, was found to be insignificant compared to the other cues. In other words, in our case, the robotisation of the animal model did not alter animals' response. This result again suggests that even robots with very rudimentary capabilities can provide insights into the animal behaviour. Experimental setups of animal-robot interactions do not necessarily require complicated robots with advanced sensor capabilities and high degree of autonomy.

An interesting, albeit rather hypothetical, parallel can be drawn with the now well-established field of human-robot interactions where the prevailing “uncanny valley” theory argues that the humanoid robots displaying only some key features are found to be more appealing to people than the ones closely resembling humans [53, 54]. Some minimal design interactive robots have shown to effectively facilitate the exchange of attention and emotion with people [20]. Extracting crucial elements that represent appearance and behaviour thus permits building robots that are both more socially acceptable and less complex. Similarly, the goal of designing robots for animal interactions can follow an equivalent rationale.

Robots that can carry sensors to observe fish at close range are useful in a wide range of applications, including species and fish size information for fishery

activities and stock management purposes, fisheries oceanography, marine ecology, and behavioural ecology. However, probing platforms or autonomous underwater vehicles may disturb fish and alter their behavioural patterns [55] which may cause bias in the observations, and designing a robot that blends in with the school will become a valuable tool. Although the performance (speed) of robots is improving [39, 42, 43], neither conventional propeller driven underwater vehicles [40] nor biomimetic underwater robots can keep up with the mackerel's swimming speed [41]. However, our study shows that a slow moving object may be able to penetrate and observe within a school, and that features like biomimetic tail motion is not a key design feature. The school's moderate responsiveness to the robot's size is also important in this context as miniaturization is one of the hardest design restrictions of autonomous underwater vehicles. For the current state-of-the-art of biomimetic underwater robots, this is an important design consideration.

In conclusion, our study contributes to the current knowledge on the efficiency of the robotic animal technique in animal behaviour research by providing evidence of its capability to simulate either social or predator-prey interactions in large scale animal aggregations. In the future, modulating the behaviour of animals using robots could facilitate aquaculture, improve animal welfare, control of the population size and permit (re)introduction of species to their natural habitats.

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Figure 1. Schematic representation of the housing net pen and experimental apparatus. An upward-looking 120 kHz split-beam echosounder (Simrad EK 60) was placed at the bottom of the experimental pen to monitor the school distribution and general swimming pattern. A horizontally-looking high-resolution imaging sonar, ARIS (Adaptive Resolution Imaging Sonar), operating at 3 MHz, was mounted on one side of the net pen at a 1 m depth to observe the school collective reactions towards the fish robots.

Figure 2. 3D model of the robotic mackerel and the smaller physical robot

Figure 3. Two examples of collective reactions exhibited by the mackerel school when exposed to the fish robots: a) evasive fountain effect and b) collective following response. The snapshots were obtained in ARISFish software from high-resolution imaging sonar (ARIS) recordings. The position of the robot is marked with a white circle. In the rightmost snapshots the robot has already left the sonar's field of view.

a)

b)

Figure 4. Experiment 1. Probability of a collective avoidance reaction exhibited by the fish school in function of a) the size and b) tail-beat motion of the fish robots. The bars represent mean values and the error bars SD values.

Figure 5. Experiment 1. Probability of a collective following responses exhibited by the fish school in function of a) the size and b) tail-beat motion of the fish robots.

Figure 6. Experiment 2. Probability of a collective avoidance reaction exhibited by the fish school in function of a) the size and b) speed of the fish robots.

Figure 7. Experiment 2. Probability of a collective following responses exhibited by the fish school in function of a) the size and b) speed of the fish robots.