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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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Supplementary material for this article is available online

Abstract

So far, actuated fish models have been used to study animal interactions in small-scale controlled experiments. This study, conducted in a semi-controlled setting, investigates robot[5] interactions with a large wild-caught marine fish school (~3000 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 and sonar-video blind scoring, we monitored and classified the school's collective reaction towards the fish robots as attraction or avoidance. We found that two key releasers—the size and the speed of the robotic fish—were responsible for triggering either evasive reactions or following responses. At the same time, we found fish reactions to the tail motion to be insignificant. 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.

Robotic models are used in animal-behaviour research to advance our understanding of social interactions and to provide guidance for manipulation of animal behaviour. Yet, the 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.

Many studies exploring the collective behaviour of fish have employed robotic-animal models in laboratory settings. These studies have permitted the accumulation of important knowledge not only on how fish perceive and react to robots, but also on how shoaling fish make collective decisions in general (Ward *et al* 2008, Faria *et al* 2010, Swain *et al* 2012). Notably, a significant endeavour has been directed at determining which key features of robotic model are responsible of triggering the social responses of fish. For example, tail undulations of interacting robotic fish increased attractiveness in zebrafish (*Danio rerio*) (Polverino *et al* 2012). It has also been found that golden shiners (*Notemigonus crysoleucas*) preferred to spend time in the vicinity of a robotic fish when its tail was beating (Marras and Porfiri 2012). Golden shiners were also found to be more attracted to a robotic fish when the robot's colour pattern matched that of real conspecifics and when the robot tail was beating at a similar frequency (Polverino *et al* 2013). In (Landgraf *et al* 2012) realistic eyes have been found to increase

[5] 'robot' is here defined as a programmable machine playing preprogrammed actuation sequences.

the attractiveness of the robotic fish. Together, these findings suggest that flow cues play an important role in shaping fish–robot interactions, most probably due to hydrodynamic advantages of swimming in the wake of companion fish (Polverino *et al* 2013, Hemelrijk *et al* 2014). However, another study in zebrafish reported that, although matching the aspect ratio and visual appearance (colour and stripes) of robot fish increased its level of attractiveness, tail-beat frequency of the robot only played a marginal role (Abaid *et al* 2012). This study was conducted in placid water without motion of the robot and it is not clear how well it holds in the case of a moving robot or moving water. In addition, the swimming speed of a robot or a group of robot fish was found to modulate the collective behaviour of focal shoaling fish (Butail *et al* 2013, Butail *et al* 2014). Despite the growing body of evidence suggesting the attractiveness potential of robots, Polverino and Porfiri (2013) found that mosquitofish were not attracted by bio-inspired robotic fish and the degree of repulsiveness varied with depth and aspect ratio. Landgraft et al. (2016) have found that realistic eyes and natural motion have increased the attractiveness for robotic fish.

Based on the above laboratory studies, it appears that the size, aspect ratio, colourization and colour pattern, tail motion or speed of robots are all important in triggering fish responses. Yet, the conclusions of these studies seem to depend on the species model, experimental setup and the type and characteristics of the robots employed.

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 (Tinbergen 1948). From an engineering point of view, Tinbergen's hypothesis also offers a possibly very appealing minimal design paradigm for robots, which is widely recognized when designing robots for interaction with humans (Kozima *et al* 2009). It suggests that to trigger the reaction of 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.

This paper will test some candidates of possible key releasers based on evidence in previous research. The importance of the biomimetic locomotion of the tail is explained by a sensitive lateral line organ that can sense the undulating motions created by other fish (or robots) (Mogdans and Bleckmann 2012). 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 (Dill 1974, Meager *et al* 2006, Turesson *et al* 2009, Seamone *et al* 2014). 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 (Krause and Godin 1994). 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 (Domenici 2001). Predators' size and velocity were found to affect the distance at which zebra danios (*Brachydanio rerio*) initiate an evasive reaction (Dill 1974), with larger and faster predators inducing greater escape responses. 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. This has recently even led to open-source software for easy implementation for testing and modular design (Landgraf *et al* 2014). 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 (Krause *et al* 2000). 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 it's tail is beating (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.

Methods

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 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

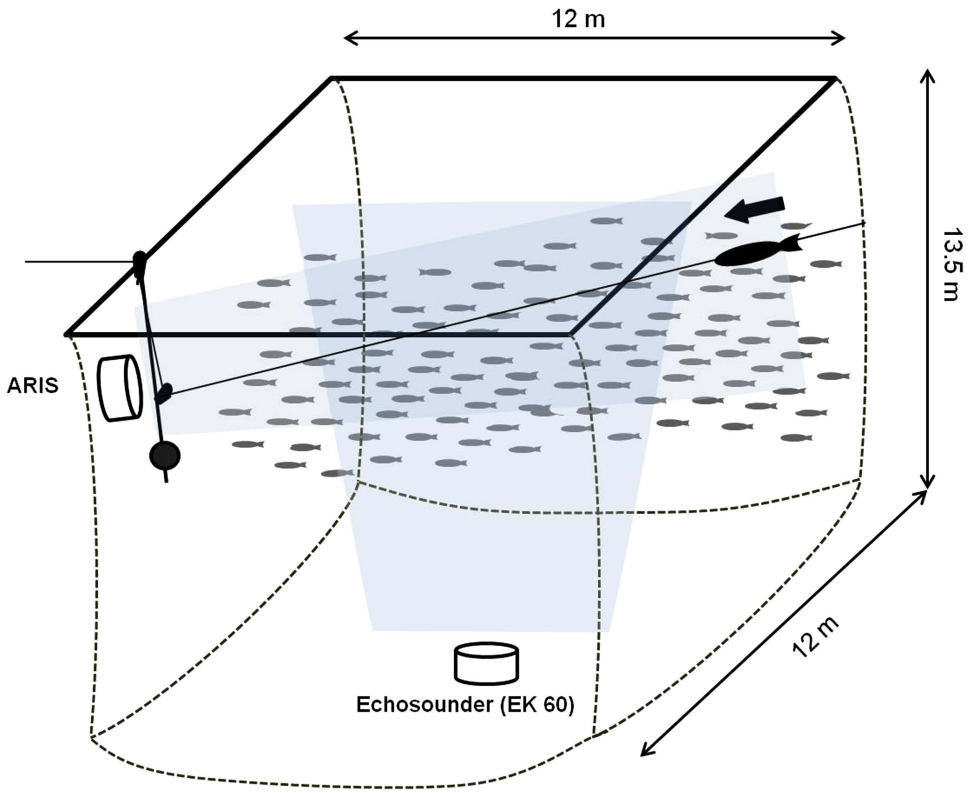

Figure 1. Schematic representation of the housing net pen and experimental apparatus. An upward-looking 120 kHz split-beam echosounder (Simrad EK 60) was placed at the bottom of the experimental pen to monitor the school distribution and general swimming pattern. A horizontal-looking high-resolution 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's collective reactions towards the fish robots.

displaying coordinated manoeuvres in response to environmental perturbations or when under a predator's attack. *S. scombrus* is a voracious fish species and an important consumer of zooplankton (Prokopchuk and Sentyabov 2006) forming schools that can reach sizes up to several millions of individuals generally organized in size-classes (Lockwood 1988). In the Northeast Atlantic, mackerels are commonly preyed upon by large marine mammals such as killer whales (*Orcinus orca*) (Nøttestad *et al* 2014).

The experiments described in this article were conducted 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 × 12.5 m wide × 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 two months prior to the experiments to allow them to acclimate to their captive conditions. The 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. The total length and weight of the fish were measured before the experimental period, $N = 19$; body length $= 41.05 \pm 2.82$ cm;
weight $= 715.37 \pm 148.3$ 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 vertical distribution of fish in the water column and to estimate the number of fish in the pen using echo integration (MacLennan and Simmonds 2005). The data collected were imported in Echoview 5.2 (Sonar-Data 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 (Maclennan *et al* 2002)) over the vertical fish distribution (NASC $= 18\,163$ m^{2}n.mi^2). By assuming a uniform horizontal distribution across the 12 m × 12 m pen ($A = 144$ m^2) and a target strength for 200 kHz of TS $= 20\log10(41) - 80$ dB re 1 m^2 (Egil Ona, pers. comm.), which gives $\sigma_{bs} = 2.11.10^{-11} m^2$, the number

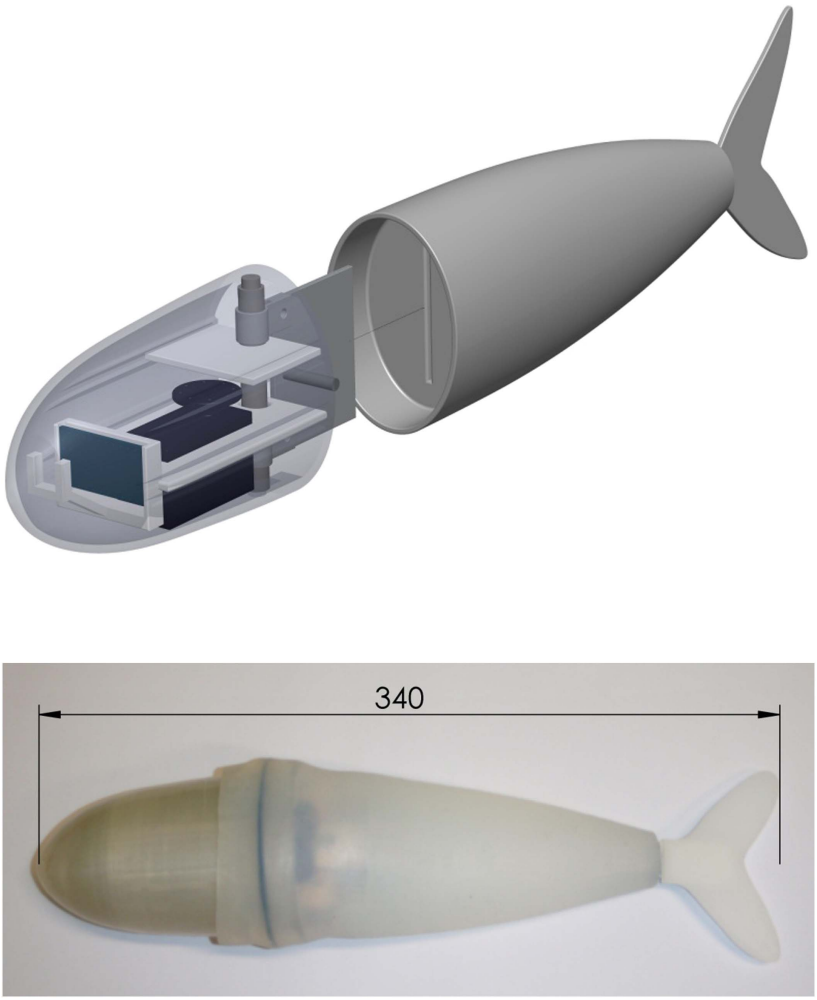

Figure 2. 3D model of the robotic mackerel and the smaller physical robot.

of fish inside the pen was estimated to be $N = NASC \cdot A \cdot (\sigma_{bs} 1852^2 4\pi)^{-1} \approx 3000$ individuals and a biomass of approximately 2 metric tonnes.

A horizontal-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's collective reactions towards the fish robots. The sonar imaging recordings were imported into ArisFish software (Sound Metrics Corporation, Bellevue, WA, USA) to analyse fish reactions.

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-sized robot was chosen based on typical mackerel sizes from commercial catches in the area. Both models where built with a 3D-printed rigid head housing the electronics and actuator, and a soft, silicone tail, cast with the help of a 3D-printed mould. 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. The locomotion of the robot mimicked subcarangiform swimming with 1/3 of the body being rigid and the rest of the body was actuated by a single servo motor. The kinematics of the tail correspond to the kinematics of a subcarangiform swimmer at cruising speed (Salumäe and Kruusmaa 2011). We expected that the wakes created by similar kinematic tail envelopes would be similar and that the robots create a comparable wake to the real mackerels.

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

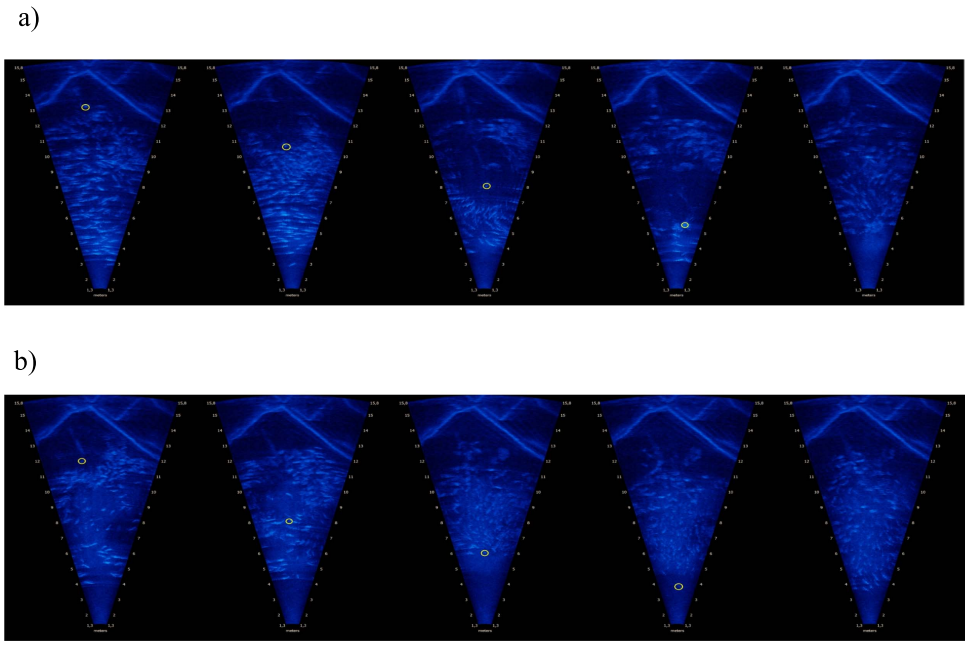

Figure 3. Two examples of collective reactions exhibited by the mackerel school when exposed to the fish robots: (a) evasive fountain effect and (b) collective following response. The snapshots were obtained in ARISFish software from high-resolution imaging sonar (ARIS) recordings. The position of the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

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 ± SD).

During our tail-beat experiment the tail-beat was roughly matched with the measured tail-beat of mackerel 1.93 ± 0.52 (mean ± SD) and a slightly lower frequency of 1.8 tail-beats per second was used for the robot (for the convenience of programming the servo motors). The amplitude of the tail-beat is expressed by the lateral movement of the caudal fin from one side to another. The approximate amplitude of the tail was calculated for both robots using results from (Bainbridge 1958) and adjusted by trial and error in water. An amplitude of 8 cm was used for the smaller model and 12 cm for the bigger model.

Both 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 arrival end of the pen (figure 1). The fishing line was connected to an electric engine placed at the opposite side of the net pen, allowing the towing speed to be precisely controlled. The speeds were recorded by timing the tow duration and were consistent between trials. A total of six random experiments were used to determine the robot's speed. A pulling speed of 0.75 ± 0.01 metres per second for the slow experiment and a speed of 1.66 ± 0.03 metres per second for the fast experiment were used (mean ± 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.

Sonar measurements

Using a high-resolution imaging sonar, we observed mackerels' two 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 afterwards regroups behind it (Pitcher and Parrish 1993) (figure 3). An attraction response is defined as the dynamic swimming of fish in the direction of the robot model.

Video scoring

We employed a qualitative approach (i.e. blind scoring) to categorize the nature and magnitude of mackerels' collective reactions towards the different robotic models. Despite recent development of techniques to quantify dynamic collective manoeuvres, information transfer and interactions between individuals in schooling fish (see (Rieucau *et al* 2016) and (Handegard *et al* 2012), we adopted a qualitative approach because our principal objective was to explore whether particular intrinsic characteristics of robotic models triggered collective responses of schooling fish in a social context close to what these fish experienced in nature, therefore, making a qualitative categorization of the collective reactions sufficient. Blind scoring of videos is a common method in

behavioural analysis in humans and non-humans (Meltzoff 1996, Stockman *et al* 2014, Tuyttens *et al* 2014). Blind scoring of underwater videos has been successfully employed in a recent study to describe school reactions of pelagic fish in a similar experimental setup (Handegard *et al* 2012).

First, we code-named all the acoustic videos of the two experiments with random numbers before the blind scoring procedure by an observer unaware of the treatments or experimental design. For each mackerel–robot encounter, the observer noted from the recorded sonar video if a behavioural reaction occurred (coded as 1) or not (coded as 0). In the occurrence of a noticeable reaction, the collective reaction was classified as fountain effect or collective attraction. For each type of reaction, the observer qualitatively determined the strength of the reaction (weak or strong). A strong reaction was defined as the uniform response of the whole fish school, whereas a weak reaction was defined as the noticeable local reaction of one or a few fish to the robot without triggering any change of the swimming pattern for the fish further away (absence of a wave of reactions through the school). During a weak response the imaginary border of the fish school stayed intact, contrary to a strong reaction which induced the temporary transformation of the shape of the fish school (a wave of behavioural responses through the school).

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, and blind scoring of recorded sonar videos. Our experimental procedure prevented habituation to a sequence of stimuli as the randomized order of presentation of the treatments (robot models and fishing line alone) made the timing of presentation and characteristics of the simulated threat unpredictable for our schooling mackerels.

The schooling fish were exposed to each combination of stimuli (size $\times$ tail-beat frequency) 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 min 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 were released using an aquaculture automatic feeder close to the surface 2 min 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 ensured 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 four consecutive blocks where two consecutive blocks were separated by at least 20 min. During a block, schooling fish were exposed to each combination of stimuli (size $\times$ 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 min to allow the fish to return to a similar schooling dynamic as prior to exposure. An observer (GR) verified that the fish returned to a 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 min before the release of the robot fish. A total of 32 exposures were conducted during this experiment.

Data 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 pseudo-replication (Hurlbert 1984), 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 (similar to (Rieucau 2014)). In addition, the randomized-block experimental design was employed in both experiments where the presentation order of the different stimuli was randomized and the interval of time between consecutive exposures may have

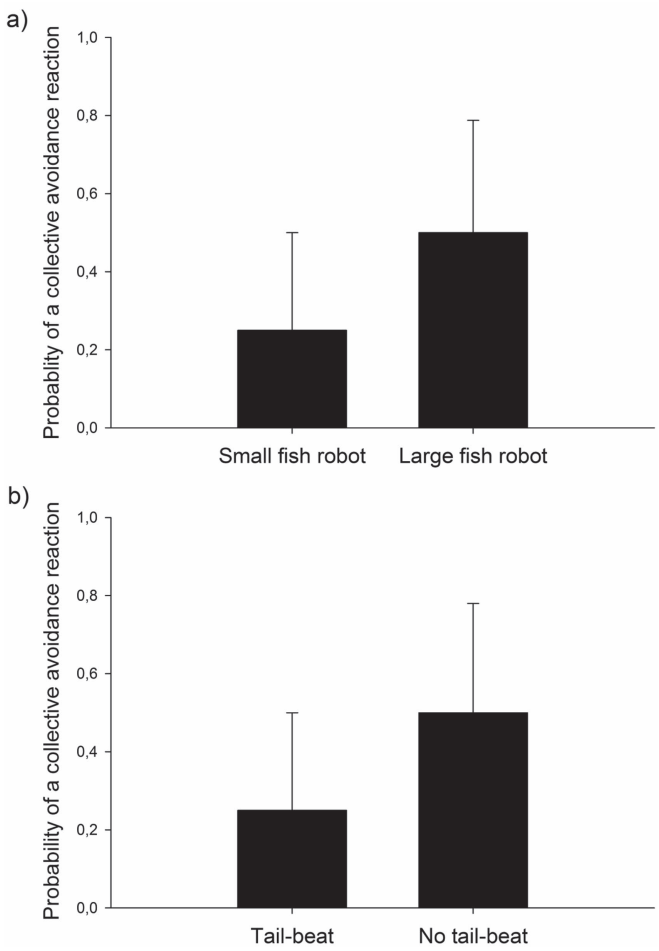

Figure 4. Experiment 1. Probability of a collective avoidance reaction exhibited by the fish school in relation to (a) the size and (b) tail-beat motion of the fish robots. The bars represent mean values and the error bars SD values.

prevented habituation and a sequence effect in responsiveness, as suggested by (Schleidt *et al* 1983). 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.

Results

Experiment 1: fish-robot biomimetic locomotion

We did not find a significant effect of the size of the robots (GLZ: Wald $\chi_1^2 = 0.63$, $P = 0.43$) or their tail-beat frequency (GLZ: Wald $\chi_1^2 = 0.54$, $P = 0.46$) 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 $\chi_1^2 = 1.09$, $P = 0.29$).

Tail-beat frequency did not influence mackerels' propensity to follow the robots (GLZ: Wald $\chi_1^2 < 0.001$, $P = 1$) (figure 5). However, even though it failed to reach the conventional level of statistical significance (GLZ: Wald $\chi_1^2 = 3.45$, $P = 0.06$), we observed a pattern towards a higher propensity of mackerels to follow the larger fish robot than the smaller; and this occurred independently of the robots' tail-beat frequency (figure 5(a)). The interaction between size and tail-beat was not statistically significant (GLZ: Wald $\chi_1^2 < 0.001$, $P = 1$).

Experiment 2: fish robots' size versus swimming speed

Both the size (GLZ: Wald $\chi_1^2 = 4.47$, $P = 0.03$) and the speed (GLZ: Wald $\chi_1^2 = 4.86$, $P = 0.03$) 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 $\chi_1^2 < 0.001$, $P = 0.99$). The larger fish robot induced significantly more avoidance reactions than the smaller one (figure 6(a)). In addition, a speedy robot fish was more effective at eliciting an avoidance reaction than a slow model (figure 6(b)).

We found a significant effect of the size of the fish robot (GLZ: Wald $\chi_1^2 = 11.30$, $P < 0.001$) and the speed at which it crossed the school (GLZ: Wald $\chi_1^2 = 12.35$, $P < 0.001$) on the probability of a mackerels' following reaction towards the robot. Regarding the robot's size, mackerels followed the small robot more than the larger one (figure 7(a)). Schooling

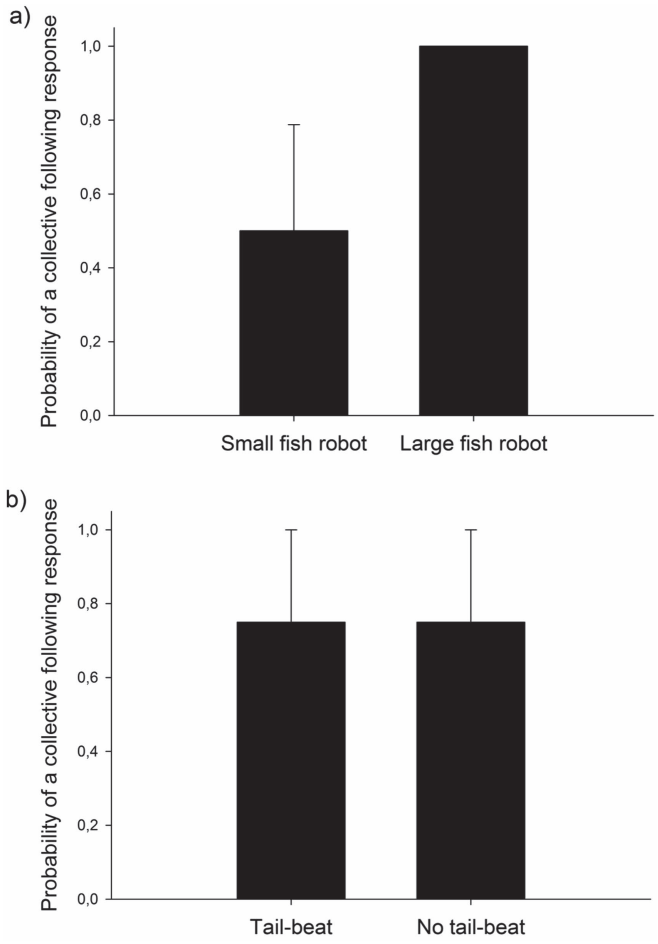

Figure 5. Experiment 1. Probability of a collective following response exhibited by the fish school in relation to (a) the size and (b) tail-beat motion of the fish robots.

mackerels followed a slow-swimming fish robot more than a speedy one (figure 7(b)). 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.

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 (~3000 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 into 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 the size and speed of the fish robots strongly affected mackerels' 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 collective avoidance behaviour in fish.

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 (Polverino *et al* 2012) and golden shiners (Marras and Porfiri 2012) in controlled laboratory conditions. In both these studies, the biomimetic locomotion was found to be the key feature determining the fish responses. However, as Abaid *et al* (2012) found no effect due to the tail-beat, it is likely that the effect of hydrodynamic cues is not that simple.

Mackerels are voracious predators and it is possible that the following responses were triggered by the fish's motivation to feed. This result is supported by the observations that small and fast-moving robots

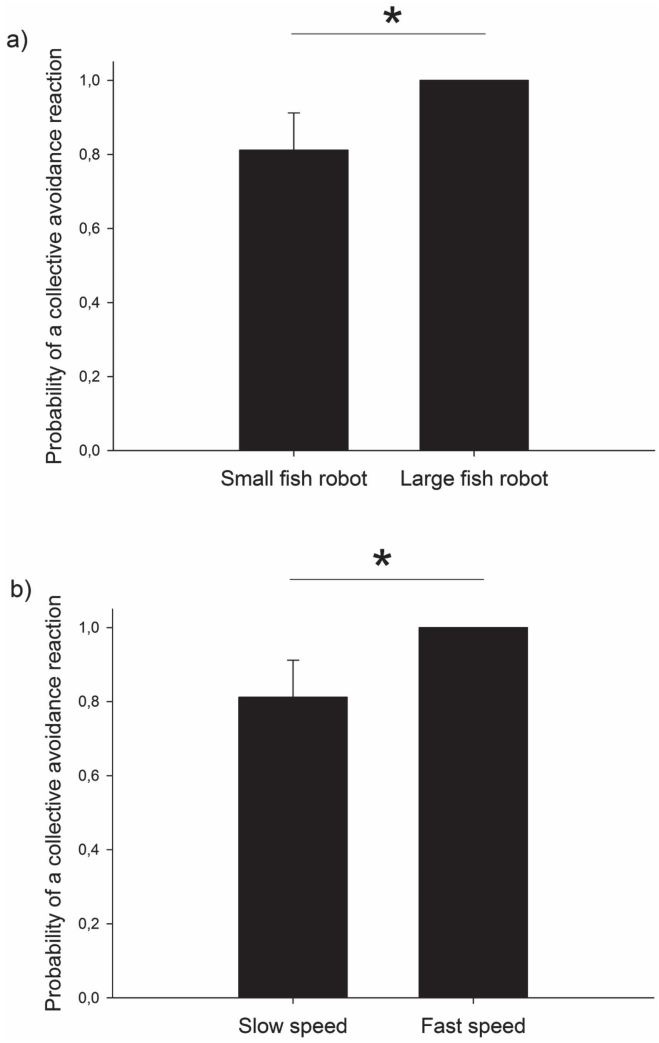

Figure 6. Experiment 2. Probability of a collective avoidance reaction exhibited by the fish school in relation to (a) the size and (b) speed of the fish robots.

increased the likelihood of collective following responses towards the robotic fish.

In water, every moving object leaves a wake behind it (the no tail-beating robot as well). Mechanistically, it is possible that the observed following responses in our experiments could have been triggered by hydrodynamic cues generated by the robotic fish whereas the wake created by the moving tail only had a marginal effect on the collective responses of the fish. An alternative explanation is that, despite of our attempt to design a robot moving in similar fashion to mackerels, the robotic fish failed to produce essential hydrodynamic cues that would have made mackerel recognize the robots as conspecifics (as we kept the tail-beat frequency constant during all experiments, but changed the speed, it is hypothetically possible that fish would have reacted differently if the tail-beat frequency increased with the speed). In this case, the following behaviour may have been triggered instead by visual cues and feeding motivation. If the ecology of the focal species and the artificial social conditions in which fish have been tested can partially explain the discrepancies in the conclusions of previous laboratory studies (in particular, regarding the effect of tail-beat), our study highlights that fish may act on different sensory cues when in noisy natural conditions and/or when swimming in large shoals.

Additionally, it remains an open question whether the robots used in our study were recognized as threats. In a previous study for example, based on the observed collective responses of zebrafish towards a swimming robot that conserved colouration, aspect ratio and carangiform/subcarangiform-like locomotion, Butail *et al* (2013) argued that it is unlikely that the robot was perceived as a predator. At the same time, in a previous sea-cage experiment, schooling herring were found to perform classical diving anti-predator reactions when exposed to a bottle-shaped predator model crossing a school at a constant speed (~3.40 m s^{-1}) (Rieucau *et al* 2014). In their natural environments, mackerels are mostly preyed upon by large marine mammal predators such as killer whales (Nøttestad *et al* 2014) that generally form highly coordinated hunting groups. In our study, the constant

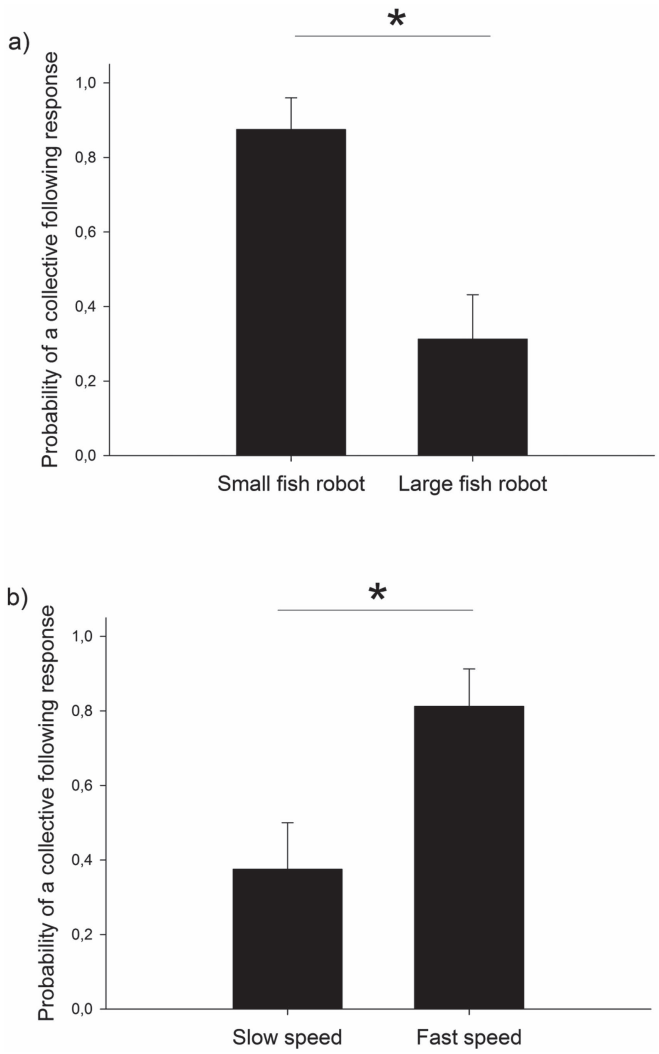

Figure 7. Experiment 2. Probability of a collective following responses exhibited by the fish school in relation to (a) the size and (b) speed of the fish robots.

speed at which the robots crossed the school may correspond to the speed of a gliding phase during attack by a solitary predator. In contrast, Atlantic herring that also aggregate in massive pelagic schools are often predated by solitary predators such as cod or saithe (*Pollachius virens*). However, it is possible that our robots may not have fully mimicked natural predators of mackerels and may not have been recognized as a direct threat, despite the fact that they demonstrated collective reactions.

In the above-mentioned sea-cage experiment on a large Atlantic herring school (*Clupea harengus*) of approximately 60 000 individuals, (Rieucau *et al* 2014) reported that 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. In our study, the colour and aspect ratio of the robot was kept constant and it remains to be a subject of future studies to investigate if manipulation of those characteristics would also alter the school behaviour. However, from the experiments performed we conclude that keeping those features constant still permits us to manipulate the collective response of the fish.

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 on fish reaction which, contrary to expectations, was found to be insignificant compared to the other cues. In other words, in our case, the robotization of the animal model did not alter animals' response. This result again suggests that even robots with very rudimentary capabilities can provide insights into animal behaviour. Experimental setups of animal–robot interactions do not necessarily require complicated robots with advanced sensor capabilities and a high degree of autonomy.

Robots that can carry sensors to observe fish at close range are useful in a wide range of applications,

including gathering 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 (Stoner *et al* 2008) 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 (Krause *et al* 2011, Liang *et al* 2011, Clapham and Huosheng 2014), neither conventional propeller-driven underwater vehicles, or biomimetic underwater robots can keep up with the mackerel's swimming speed (Wardle and He 1988). However, our study shows that a slow-moving object may be able to penetrate and observe a school, and that features like biomimetic tail motion are 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 greatest design restrictions of autonomous underwater vehicles. For the current state-of-the-art of biomimetic underwater robots, this is an important design consideration.

A possible future research direction could also be the response of the fish school to multiple robots. (Butail *et al* 2014) offer some insights in a laboratory setting into how speed and distance between the robots could be used to manipulate fish behaviour. Again, it would be interesting to find out if those findings hold in a noisy natural environment.

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, improve control of the population size and permit the (re)introduction of species to their natural habitats.

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