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RESEARCH ARTICLE

Angling gear avoidance learning in juvenile red sea bream: evidence from individual-based experiments

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ABSTRACT

Angling gear avoidance learning is a possible factor that contributes to the vulnerability of caught-and-released fish to angling. Whereas past studies suggested angling gear avoidance learning, they were based on large-scale experiments on groups of fish and unable to verify learning accurately. Details of avoidance learning are also unclear. The present study investigated angling gear avoidance learning through a series of individual-based experiments using red sea bream (*Pagrus major*) juveniles. Fish avoided angling gear after only one or two catches while showing feeding motivation for pellets, representing avoidance learning for angling gear. Most of the experienced fish avoided krill attached to a fishing line, but not krill alone or pellets presented near the angling gear. Experienced fish were less vulnerable to angling than control fish. Approximately half of the experienced fish kept the memory of angling gear 2 months after learning. The learning effect through the catch-and-release procedure would reduce catchability and the value of fishery-dependent stock assessments.

KEY WORDS: Fishing, Catch and release, Cognitive ecology, Conditioning, Memory, Preparedness

INTRODUCTION

Catch-and-release angling is known to reduce angling mortality and is often practiced for the management of fish resources (Muoneke and Childress, 1994; Pollock and Pine, 2007). However, some studies have shown that repeated captures of the same individuals can increase the risk of mortality (Bartholomew and Bohnsack, 2005; Levin et al., 2018), or at least cause physiological damage, behavioural change and stress to fish (Davis et al., 2005; Brownscombe et al., 2017). It is thus necessary to investigate how catch-and-release angling affects the vulnerability of released fish to angling in order to accurately evaluate the effectiveness of catch-and-release angling for resource management.

A possible factor that contributes to the vulnerability of released fish to angling is angling gear avoidance learning, i.e. the ability of fish to learn to avoid angling gear through the experience of being hooked and caught (Beukema, 1970a; Fernö and Huse, 1983; Klefoth et al., 2013; Lennox et al., 2017). Some studies have suggested angling gear avoidance learning under large-scale conditions, showing that catch rates in natural conditions and fishponds declined over time through the experience of being captured (Beukema, 1969; Alós et al., 2015). However, these past studies on angling gear avoidance learning were based on large-scale experiments on groups of fish in ponds or large experimental tanks, and were unable to confirm the feeding motivation of each individual fish before they avoided angling gear, implying that the fish might have been demotivated to feed owing to stress from the angling experience (Siepker et al., 2006; Stålhammar et al., 2012), not by angling gear recognition. In addition, in large-scale experiments, naive fish may be misidentified as learned fish owing to group interactions, and vice versa. For example, because aversive experience often enhances the alertness of fish (Takahashi and Masuda, 2018), captured fish can become more cautious than naive fish. Cautious fish tend to eat less willingly than bold fish (Klefoth et al., 2013) and thus can become less vulnerable to angling, which might be misinterpreted as a sign of avoidance learning. Conversely, because competition in a shoal of conspecifics often increases their feeding motivation (Stoner and Ottmar, 2004; Pfeiffenberger and Motta, 2012), even learned fish may strike angling gear and might be recorded as naive fish.

Moreover, many questions remain unanswered regarding angling gear avoidance. For example, it is unclear how many times fish need to be captured to establish angling gear avoidance learning. Beukema (1969) found through experiments with carp in artificial ponds that many fish became invulnerable to angling after being caught once; however, that study did not rule out the possibility of reduced feeding motivation. It is also uncertain how long learned avoidance of angling gear is retained because the only reference available is a study in large ponds (Beukema, 1970b), in which the feeding motivation of caught fish was not confirmed. In addition, it has not been investigated which part of the angling gear is recognised for avoidance learning. This question is worth examining because angling gear avoidance learning can have positive or negative effects depending on which part of the angling gear fish recognise as dangerous; for example, if fish recognise bait as dangerous, learned avoidance behaviour might affect their food intake. Furthermore, it is unknown to what extent angling gear avoidance learning contributes to invulnerability to angling.

The present study investigated angling gear avoidance learning through a series of small-scale experiments (a single fish in a tank) with hatchery-reared red sea bream (*Pagrus major*) juveniles. Red sea bream at the adult stage is targeted for professional pole-and-line fishing and recreational angling (Shishidou, 2002). In particular, the juveniles are often targeted for both commercial and recreational fishing in coastal zone. However, they are released owing to size limitations by fishery adjustment rules (Isshiki, 2013). They are thus likely to have a chance of learning how to avoid angling gear during their life.

In experiment 1, we conducted catch-and-release angling on individual fish for 28 consecutive days to investigate whether and how fast fish can learn to avoid angling gear and observe behavioural

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changes towards angling gear over the duration of the experiment. In experiment 2, we exposed experienced fish to different sets of angling items to investigate which part of the angling gear was recognised for avoidance learning. In experiment 3, we compared catch rates between experienced and naive fish to estimate the effect of avoidance learning on vulnerability to angling. In experiment 4, we examined the long-term retention of learned behaviour. Each experiment was conducted on an individual basis using separate experimental tanks to eliminate the effect of group interactions. Before every test or trial, fish were tested for feeding motivation using pellets, which enabled us to distinguish between avoidance learning and decline in feeding motivation. Through these experiments, we aimed to address the above-mentioned questions and provide detailed insight into angling gear avoidance learning.

MATERIALS AND METHODS

Materials

Fertilized *Pagrus major* (Temminck & Schlegel 1843) eggs (approximately 20,000 eggs), purchased from Marua Suisan Co., Ltd (Ehime prefecture, Japan), were transported to the Maizuru Fisheries Research Station, Kyoto University, and kept in 500-liter transparent polyethylene tanks under natural light conditions. Water in each tank was exchanged at a rate of 4 l min^{-1}, and an aeration was set in the tank. Seawater used for the rearing tanks was pumped from off the research station and fine-filtered. The water temperature was maintained at 20°C using a heater and thermostat. After hatching on 17 May 2013, larvae were fed with rotifer *Brachionus plicatilis* sp. complex (approximately 5 ind. ml^{-1}), brine shrimp *Artemia* sp. nauplii (approximately 2 ind. ml^{-1}) and dry pellets (Otohime B1, Otohime C2 and Otohime S2, Marubeni Nisshin Feed Co., Ltd) in an amount corresponding to the growth. Fish were reared for at least 9 months in the stock tanks.

Out of these hatchery-reared red sea bream juveniles, 22 were used for experiments (body length: 118.3±10.8 mm, mean±s.d.). Eleven blue polypropylene containers (45×66×33 cm, width×length×depth, water depth 25 cm) were used as experimental tanks. A single fish was introduced in each tank and acclimatised to twice-daily feeding (i.e. in the morning and evening) for at least 3 days. Experiment 1 was initiated after confirming that the fish ate pellets within 30 s during the morning feeding period.

Ethical notes

All experiments were performed according to the regulations on animal experimentation of Kyoto University, and guidelines for the use of fishes in research by The Ichthyological Society of Japan. A minimum number of fish was used to test the hypotheses. After the experiments, the fish were donated to a local aquarium.

Experiment 1: acquisition of angling gear avoidance and behavioural change through learning

We conducted catch-and-release angling on individual fish for 28 consecutive days to investigate whether and how fast fish can learn to avoid angling gear. A daily trial for each individual consisted of a feeding motivation test and an angling test. In the feeding motivation test, three to four pellets were presented to the fish. After confirming that the fish ate the pellets within 30 s, i.e. that the fish had feeding motivation, the angling test was immediately conducted. The confirmation of feeding motivation prior to catch-and-release angling enabled us to distinguish between avoidance learning and decline in feeding motivation.

The fish were divided into angling and control treatments (11 fish for each treatment). Angling treatment fish were each exposed to angling gear, and feeding behaviour on bait was observed for up to 60 s. A device of terminal tackle was used as angling gear, consisting of a rod (approximately 90 cm in length), a fishing leader tied at one end to the tip of the rod, a fishing sinker attached to the other end of the fishing leader, and a single hook with a line (approximately 5 cm in length) tied to the fishing leader. The barb of the hook was pressed by pliers to reduce the stress of hooking and releasing. Defrosted krill was cut into pieces of approximately 5–8 mm, and one of the pieces was put on the hook as bait. As soon as a fish took krill with the hook in the mouth, the fish was quickly pulled out of the water through the fishing leader, which was recorded as a ‘catch’. The caught fish was kept in air for at least 30 s, and then returned to the experimental tank after the hook was removed from the snout. When it was difficult to remove the hook from the mouth, the fishing leader was cut with the hook left in the mouth, which did not affect the feeding motivation of the fish according to the observation of feeding in the next feeding motivation test. If the fish did not eat krill for 60 s, the angling test was terminated and recorded as ‘no catch’. The fish sometimes pecked and took krill away without being hooked, which was recorded as ‘biting’. In this case, another piece of krill was attached to the hook to continue the angling test. Control fish were exposed to the same gear as angling treatment fish, except that the end of the hook was cut off with pliers so as to allow them to eat krill without being hooked or caught. Daily trials were conducted during daytime before noon (07:00–11:00 h). To reduce individual variability in hunger level, both angling and control fish were sufficiently fed with pellets every afternoon (15:00–18:00 h). The daily trial procedure was repeated for 28 consecutive days. The treatments were replicated two times, with six angling and five control individuals in the first replicate and five angling and six control individuals in the second replicate.

We also investigated whether each individual in the angling treatment learned to avoid angling gear. When a fish avoided being caught even though it ate pellets in the feeding motivation test, the fish was considered to be learned. The number of trials that each individual required to learn was determined.

We analysed the effect of angling treatment on feeding behaviour (fed including catch and biting or not) using a generalized linear mixed model (GLMM) with the lme4 package (Douglas et al., 2015) for R v.3.6.1 (https://www.r-project.org/) statistical software. The error distributions of the response variables were fitted to the binomial distribution, using restricted maximum likelihood parameter estimation. The fixed factors were treatment (angling or control), trial (1–28 trials) and their interaction (treatment×trial), whereas individual was treated as a random factor because the feeding behaviour of each individual was repeatedly measured in 28 trials. To evaluate the behavioural change of angling treatment, the catch and feeding of only the angling treatment fish was fitted to GLMM (variable factor: angling: caught or not; feeding behaviour: fed or not; fixed factor for each variable factor: trial; random factor: individual; error distribution: binomial). Biting time was also fitted to GLMM with the error distribution of Poisson (fixed factor: trial). To evaluate feeding behaviour during avoidance, the catch rate of only the fish that showed feeding behaviour to angling gear was fitted to GLMM (fixed factor: trial; error distribution: binomial). We used the likelihood ratio test to evaluate the effect of the fixed factors for each model.

Experiment 2: cognition target for angling gear avoidance learning

We investigated the perception of angling gear by experienced fish 1 h after the last daily trial (day 28) of experiment 1. In the experiment, both angling and control treatment fish were exposed to the following sets of angling items: pellets near angling gear, krill with a line, and krill (Fig. 1). Pellets near angling gear without krill were presented to determine whether fish would decrease feeding motivation in the presence of angling gear. In the krill with a line test, angling gear was presented in the same manner as for the control treatment in experiment 1 so that fish were allowed to eat krill without being hooked. The krill test was the presentation of krill alone without angling gear for determination of whether fish would avoid the bait itself. Feeding motivation for pellets was confirmed just before each test. These presentation tests were conducted sequentially in this fixed order for each individual to reduce the number of fish used in the experiment and to decrease the effect of previous tests. Each presentation test lasted for 60 s or until the fish ate pellets or krill. Feeding rates were compared between treatments and between presentation tests for each treatment using Fisher's exact test. Latency to feed was measured for each test and compared between treatments using Student's *t*-test.

Experiment 3: comparison of vulnerability to angling between angling treatment and control

We investigated whether experienced fish can be less vulnerable to angling than control fish. One hour after the end of experiment 2, following the confirmation of feeding motivation for pellets, blind angling tests were conducted by eight persons who were not informed about the experiments. In each test, angling gear with a hook and krill was presented for 60 s in the same manner as for the angling treatment in experiment 1. Feeding behaviour was observed during the test, and latency to catch was measured if the fish was hooked. Catch rates were compared between the angling and control treatments using Fisher's exact test, and the odds ratio of capture for the angling treatment was estimated against that of the control. After the test, the fish was transferred into a beaker and photographed for measurement of body length using ImageJ software (https://imagej.nih.gov/ij/). We confirmed that there was no difference in body length between the treatments (angling treatment, 117.8±8.8 mm; control, 118.8±12.6 mm; Student's *t*-test, $t_{1,20}$=−0.19, *P*=0.84). Then, the individuals of angling treatment were transferred into rearing tanks (200-liter transparent circular tanks) prepared separately for the two replicates, and reared in the same manner as those in the stock tanks until experiment 4.

Experiment 4: long-term retention of angling gear avoidance learning

Approximately 2 months (56–67 days) after experiment 3, we investigated whether angling treatment fish retained learned behaviour (*n*=10, because one fish of the second replicate died before the experiment). On the day before the experiment, fish were introduced into separate experimental tanks to be acclimatised for a night. Then, for evaluating the retention of learning for angling gear, each fish was exposed to pellets near angling gear and krill with a line in the same manner as in experiment 2. Feeding motivation for pellets was confirmed before each presentation. Feeding rates were compared between presentation tests using Fisher's exact test.

RESULTS

Experiment 1

All the fish in both treatments ate the presented pellets in the feeding motivation tests. Thus, any lack of feeding in the presence of angling gear in angling tests was considered as angling gear avoidance learning, not as loss of feeding motivation.

In contrast, all individuals in the angling treatment avoided angling gear after one (*n*=5) or two (*n*=6) angling trials; i.e. fish required 1.6±0.5 trials (mean±s.d.) to learn to avoid angling gear (Table 1). However, all fish were recaptured within 13 days after avoidance learning (Table 1), and the total number of captures in 28 days varied from three to eight among individuals.

The GLMM analysis showed that there were significant effects of treatment and trial on feeding behaviour in both treatments (treatment *P*<0.0001, trial *P*<0.05; Fig. 2, Table 2), but not their interaction (treatment×trial *P*>0.05). For the angling treatment fish, there was a significant effect of trial in each GLMM (feeding behaviour *P*<0.01, angling *P*<0.001; Fig. 3A; number of bites *P*<0.05; Fig. 3B, Table 2). For the catch rate of the fish that exhibited feeding behaviour, there was a significant effect of trial on catch rate (*P*<0.001, Fig. 3C, Table 2).

Experiment 2

The angling treatment fish showed a feeding rate of 100% (11/11 individuals) for pellets near angling gear, 9.1% (1/11) for krill with a line, and 100% (11/11) for krill (Fig. 4). Meanwhile, the feeding rate of the control fish was 100% (11/11) for all the presentation tests.

The feeding rate for krill with a line in the angling treatment was significantly lower than that in the control treatment (*P*<0.001), but not different from the other treatments (*P*=1.00). Moreover, the

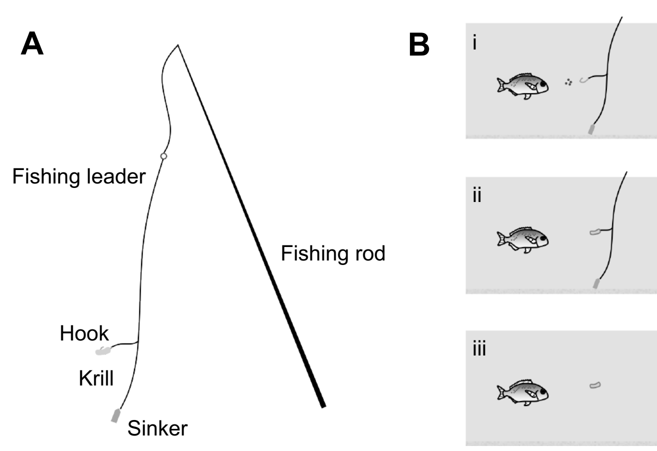

Fig. 1. Schematic illustrations. (A) Angling gear. (B) Presentation tests in experiment 2: (i) pellets near angling gear, (ii) krill with a line and (iii) krill.

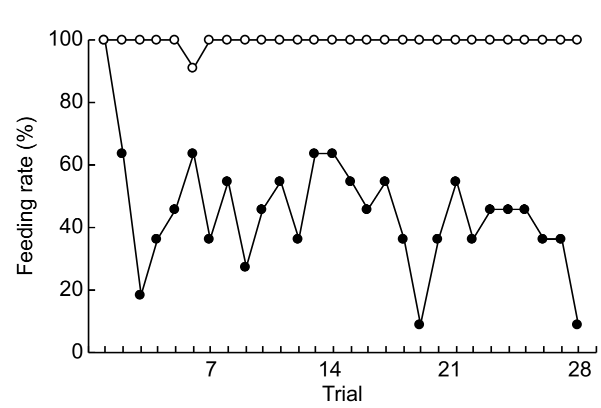

Fig. 2. The feeding rate of red sea bream in the control (open circle, *n*=11) and angling (closed circle, *n*=11) treatments in 28 trials of experiment 1.

Table 1. Data from individual red sea bream in experiments 1 to 3

Fish no.	Required trials until learning	Required days until recapture	Total catches in 28 days	Latency to eat pellets near angling gear (s)	Latency to eat krill with the line (s)	Latency to eat krill (s)	Latency to catch (s)	Cause of no catch	Standard length (mm)
Angling treatment									
1	2	6	8	4	No feed	1	No catch	Biting	126.9
2	2	3	7	2	No feed	2	18	–	119.2
3	2	2	8	17	No feed	5	No catch	Biting	119.0
4	2	2	4	7	No feed	2	No catch	Biting	97.2
5	2	7	6	8	No feed	2	No catch	No eat	131.2
6	2	13	3	3	No feed	23	No catch	Biting	120.1
7	1	5	8	1	No feed	3	52	–	115.7
8	1	1	8	2	No feed	4	No catch	Biting	124.0
9	1	2	7	4	No feed	3	No catch	Biting	116.5
10	1	4	5	7	11	2	No catch	No eat	107.7
11	1	2	6	14	No feed	3	No catch	Biting	118.4
Control									
1	–	–	–	3	3	1	1	–	114.7
2	–	–	–	8	4	3	2	–	129.5
3	–	–	–	5	4	2	6	–	122.5
4	–	–	–	3	2	2	18	–	119.0
5	–	–	–	6	3	6	32	–	100.0
6	–	–	–	1	3	2	4	–	151.5
7	–	–	–	3	3	3	3	–	109.8
8	–	–	–	2	4	1	1	–	116.1
9	–	–	–	8	2	4	No catch	Biting	114.5
10	–	–	–	2	1	1	18	–	110.7
11	–	–	–	3	6	3	No catch	Biting	118.1

feeding rate of the angling treatment fish for krill with a line was significantly lower than that for the other presentations (P<0.001). There was no difference in feeding rate between the presentation tests for the control (P=1.00). Additionally, the latency to eat krill with a line in the control (3.2±1.3 s) was faster than that (11 s) of the single fish that ate krill with a line in the angling treatment (one-sample t-test, $t_{1,10}=-19.53$, P<0.001; Table 1). In contrast, there was no difference in feeding latency between the treatments for pellets near angling gear and krill (pellets near angling gear: $t_{1,20}=-1.33$, P=0.20, krill: $t_{1,20}=-1.04$, P<0.31).

Experiment 3

The catch rate in the blind tests was 18.2% (2/11) for the angling treatment and 81.8% (9/11) for the control, and there was a significant difference in catch rate between the treatments (P<0.01; Table 1). The latency to catch was 18 and 52 s for two feeding fish of the angling treatment and 9.4±10.2 s for the control treatment, and there was a significant difference between the treatments (one-sample t-test control versus 18 s; $t_{1,8}=-2.37$, P<0.05). The cause of no catch in the angling treatment was either they did not feed at all (two individuals) or showed only biting (the other seven individuals). Two control fish showed biting for angling gear but were not caught. The odds ratio for caught fish in the angling treatment was 0.05 against the control.

Table 2. Results of the likelihood ratio test (LRT) in GLMM on experiment 1

Fixed factor	LRT	P
Both treatments		
Feeding behaviour		
Treatment	45.65	**<0.001**
Trial	6.17	**0.013**
Treatment×trial	2.04	0.15
Angling treatment		
Feeding behavior		
Trial	6.93	**0.008**
Catch		
Trial	20.1	**<0.001**
Biting		
Trial	4.6	**0.032**
Only biting fish		
Catch		
Trial	13.35	**<0.001**

Experiment 4

The feeding rate of experienced fish 2 months after the acquisition of avoidance learning was 100% (10/10) for pellets near angling gear and 50% (5/10) for krill with a line. The feeding rate for krill with a line was significantly lower than that for pellets near angling gear (P<0.04), even after 2 months of angling experiments.

DISCUSSION

To properly verify angling gear avoidance learning, the present study confirmed that the fish had enough feeding motivation before exposing individual fish to angling gear. In experiment 1, all individuals in the angling treatment ate krill from angling gear and were caught on the first trial. However, both feeding and catch rates of the angling treatment fish decreased with increasing experience of angling, while they always demonstrated active feeding for pellets in the feeding motivation tests. This result eliminates the possibility that fish were demotivated to feed by stress from angling experience, which past large-scale experiments did not exclude, and shows that the fish learned to avoid angling gear. Feeding motivation for pellets was also confirmed in experiments 2, 3 and 4, which enabled us to investigate the learning capability of fish in a reliable manner.

In experiment 1, all individuals of the angling treatment learned to avoid angling gear after only one or two catches. Red sea bream juveniles learned quickly to avoid angling gear. In a recent study that investigated the ability of red sea bream to learn to escape from net-chasing, they required more trials to acquire escape learning (Takahashi et al., 2015). Red sea bream juveniles may learn

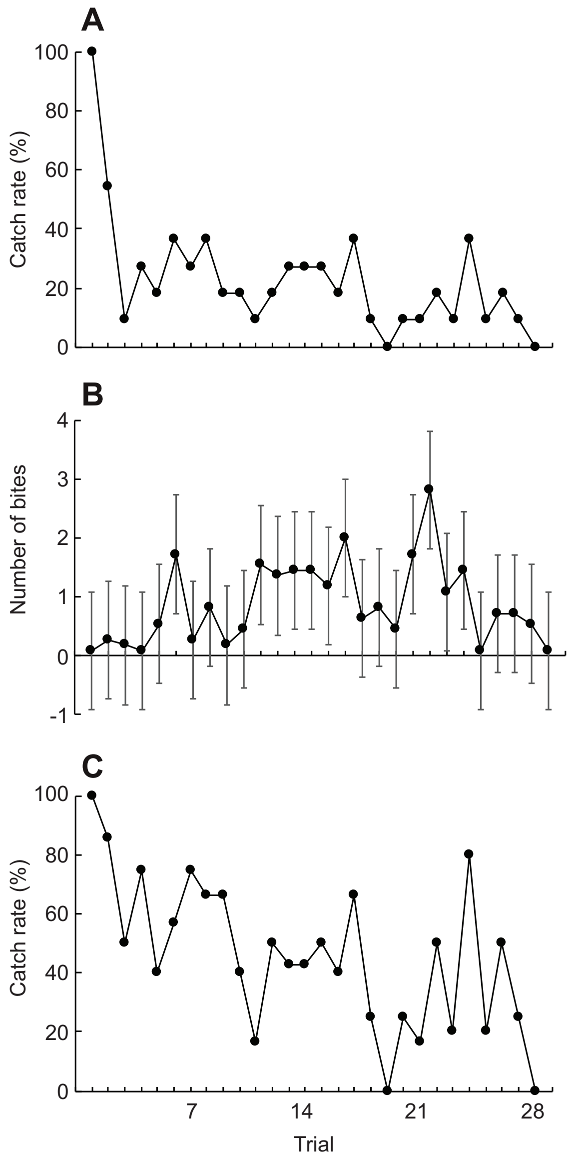

Fig. 3. Behavioural change of angling treatment fish (*n*=11) in 28 trials of experiment 1. (A) Catch rate of angling treatment fish, (B) number of bites by of angling treatment fish (bars indicate standard error), and (C) catch rate of angling treatment fish that showed feeding behaviour.

avoidance behaviour for angling quicker than they would learn to escape from a net. Being captured by angling would lead to higher mortality of fish than being chased by a net. It is predicted that learning to avoid such strong stimuli should be crucial for their survival, which may be the reason why they demonstrated quicker learning for angling.

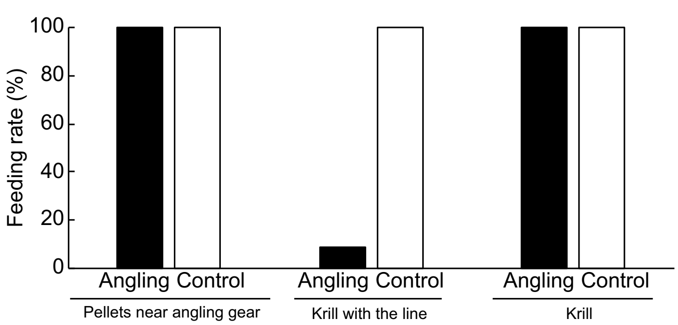

Fig. 4. The feeding rate of red sea bream in the angling (black column, *n*=11) and control (white column, *n*=11) treatments for three sets of angling items in experiment 2.

The interval of angling affects the catchability of fish, i.e. fish become less vulnerable to angling when they frequently face angling risks (Koeck et al., 2020). In this study, red sea bream encountered angling gear every day, and thus they should have acquired invulnerability to angling; if there is a greater span between angling trials, fish might have acquired less than the present study. Even though the angling treatment fish learned to avoid angling gear, on average they were caught 6.4 times out of 28 angling trials. Some studies have also reported that fish with previous experience of angling can still be recaptured (Schill et al., 1986; Tsuboi and Morita, 2004). These studies, together with our findings, indicate that angling gear avoidance learning obtained through experience does not completely eliminate the risk of recapture. Fish may be recaptured in places where anglers are abundant, such as major fishing grounds or fishing ponds, even after learning.

The fact that the angling treatment fish were recaptured several times does not necessarily mean that their learned avoidance diminished in a short period of time. The catch rate of the angling treatment fish decreased over 28 days, suggesting that avoidance learning progressed gradually as the fish repeatedly experienced angling. Meanwhile, biting behavior, namely pecking krill on angling gear without being hooked, was not completely diminished even after learning progressed, or rather the number of biting actions increased over 28 days. This means that as the fish experienced angling, they learned not only to avoid angling gear but also to steal krill from angling gear without being hooked. In fact, the catch rate of only the feeding fish decreased remarkably across trials. Improvement of feeding skills has been found in some fishes (Hughes et al., 1992; Warburton and Hughes, 2011), but the present study is the first, to our knowledge, to have observed the improvement of food stealing from angling gear.

In experiment 2, all of the experienced fish ate pellets in the presence of angling gear. Therefore, we consider that feeding motivation was not lowered by vigilance against angling gear. For the presentation of krill alone, all fish ate quickly, implying that the fish did not recognise the bait itself as a dangerous object, unlike in food aversion learning, in which fish avoid aversive food containing toxic or unpalatable substances by recognising the food itself as dangerous (Lamb and Finger, 1995; Crossland, 2001). The feeding latency of these presentations was not different between angling and control treatment fish, indicating that the experienced fish did not recognise them as dangerous subjects. In contrast, almost all fish in the angling treatment avoided krill with a line, and the feeding latency of the only feeding fish in the angling treatment was longer than that of the feeding fish in the control, which means that red sea bream juveniles evaluated the risk of angling gear on the basis of the presence of a fishing line attached to a bait. This also implies that red sea bream's perception of angling gear is based on visual cues.

The fact that red sea bream recognised krill with a line for avoidance learning would help them to survive in natural environments. Fish caught by anglers are often returned to the water, either by being released or by managing to escape. Released or escaped fish must avoid being recaptured because repeated captures would increase the risk of mortality (Bartholomew and Bohnsack, 2005; Levin et al., 2018), but they must also forage for food to live. If released or escaped fish refrain from eating in the presence of angling gear or learn to recognise some kind of food as aversive, they would lose a chance to take food even when it is safe. It would be essential for fish to properly judge the safety of food by determining whether it is attached to a fishing line so as to balance the trade-off between food intake and risk avoidance.

In the blind tests (experiment 3), the catch rate of the angling treatment fish was remarkably lower than that of the control treatment fish, with a 20-times difference in vulnerability to angling between the treatments. Although past large-scale experiments suggested decreases in catch rate associated with repeated angling experiences (Klefoth et al., 2013; Lennox et al., 2017), it is possible, for the reasons mentioned in the Introduction, that the fish had not learned avoidance behaviour or had been affected by group interactions. The present experiment verified the effect of avoidance learning on invulnerability to angling on an individual basis using the fish that had reliably learned avoidance behaviour for angling gear, and provided more convincing evidence that invulnerability to angling can be markedly improved by angling gear avoidance learning. Furthermore, learning efficiency is often enhanced by social learning (Brown and Laland, 2011; Takahashi et al., 2012). Social learning for angling gear was confirmed in Lovén Wallerius et al. (2020), and thus the acquisition of invulnerability to angling would be even quicker in natural waters than we show in the present study.

In experiment 4, approximately half of the angling treatment fish avoided krill attached to a line 2 months after experiments 1 to 3, suggesting that the fish, or at least some of them, retained learned avoidance behaviour for a long duration. Long-term retention of angling gear avoidance learning would help fish at continuous risk of recapture to survive for long periods. It is known that learned information is more likely to be retained when it is ecologically important. For example, low-growth individuals at higher risk of predators retain predator information longer than high-growth individuals at lower risk of predators (Brown et al., 2011). It might be advantageous for red sea bream to retain learned avoidance behaviour for long periods because they are exposed to the risk of recapture throughout life.

Through the individual-based experiments on red sea bream juveniles, the present study provided strong support for the hypothesis, suggested by past large-scale experiments but not verified in a reliable manner, that fish can learn to avoid angling gear. In addition, the present study addressed some of the unanswered questions about angling gear avoidance learning and obtained important findings: the red sea bream juveniles demonstrated the quick acquisition and long-term retention of angling gear avoidance learning, and the juveniles learned angling gear by identifying specific parts of the angling gear, namely krill attached to a fishing line. Such an ability would help them survive in an environment in which they would frequently encounter potential risks, including angling gears. Because the vulnerability of red sea bream juveniles to angling decreased as a result of angling gear avoidance learning, with no negative effect of avoidance learning such as decline in feeding motivation or excessive avoidance of harmless food or gear, catch-and-release angling is considered to be effective at least for the resource management of red sea bream. However, it is unclear whether other species have the same learning capability as red sea bream. In particular, species that are not targeted for angling may have different learning capabilities. As a next step, similar individual-based experiments on various species will be helpful to explore the cognition of angling gear in fish.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: K.T.; Methodology: K.T.; Validation: K.T.; Formal analysis: K.T.; Investigation: K.T.; Writing - original draft: K.T.; Writing - review & editing: R.M.; Supervision: R.M.; Funding acquisition: K.T.

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Data availability
Data are available from the figshare digital repository: https://doi.org/10.6084/m9.figshare.13499412.v1

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