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Tilting Behaviour and Its Learning in Juvenile Red Sea Bream, *Pagrus major*

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Abstract: Tilting behaviour in hatchery-reared and wild juveniles of red sea bream, *Pagrus major*, was studied experimentally. The tilting behaviour was enhanced by putting hatchery-reared juveniles under predation pressure, which showed that this predator-induced behaviour was learned. The effect was considered to be retained at least for three hours. Fish exhibiting tilting behaviour just after release into experimental tanks containing young yellowtail were harder to be targets to the attack of predators than non-tilting fish. This suggests that the tilting behaviour might function as a means of predator avoidance. Wild juveniles showed weak tendency toward tilting behaviour under predation pressure and they swam away from yellowtail. Whether an individual tilts or not seems to be due to its career on an exposure to diverse predation pressures.

Key words: *Pagrus major*, Tilting behaviour, Predation pressure, Learning

Introduction

Red sea bream, *Pagrus major*, is an economically important marine fish in Japan. Mass seedling production of this species has been developed mainly in western Japan, and the hatchery-reared seedlings have been stocked on a large scale in natural environments (Matsumiya *et al.*, 1984; Fukuhara, 1990). The annual number of seedlings stocked in recent years has been over 16 million (Japan Fisheries Agency, 1992). Despite the great effort in stocking hatchery-reared fish, little information exists on its effectiveness in fisheries after release into the sea (Fukuhara, 1990).

Predation might be responsible for the initial decrease in number just after the release of hatchery-reared red sea bream (Tsukamoto *et al.*, 1989). It has been pointed out that wild juveniles have a high ability to learn to avoid predation and their survival rate could be higher than that of hatchery-reared juveniles that have been lived in the predator-free world (Anraku and Azeta, 1973). The biological characteristics of the hatchery-reared seedlings for stocking should be modelled after those of the wild juveniles for high survivorship. Some manipulation such as exposure to predators is required during the course of rearing or before stocking (Fukuhara, 1990).

Behavioural study, which is important for understanding factors directly affecting the survival just after release in red sea bream, has just begun. Some attention has been paid to tilting behaviour which was observed in the juvenile and young stages of *P. major* in artificial conditions (Tsukamoto, 1990, 1993; Yamaoka *et al.*, 1991; Tsumura and Yamamoto, 1993; Uchida *et al.*, 1993). According to Tsukamoto (1990, 1993) and Uchida *et al.* (1993), the tilting behaviour is a behaviour in which the body is tilted motionlessly against the substratum, making redish vertical stripes on the flanks more conspicuous, and appears when the seedlings are put in artificial new environments or situations. It is considered to be a fright reaction. This behaviour was suggested to be effectual for making the survival rate higher when released into the natural environment (Tsukamoto, 1990, 1993; Uchida et al., 1993).

Recently, Yamaoka *et al.* (1991) pointed out the possibility that the tilting behaviour coud be learned by artificial seedlings under the pressure of predation. This kind of approach has been made mainly in salmonids (Kanid'yev *et al.*, 1970; Ginetz and Larkin, 1976; Patten, 1977; Olla and Davis, 1988, 1989). Our hypotheses, to be challenged in the present study, are that the tilting behaviour can be learned by the predation pressure and there exist differences in the behavioural characteristics between fish from different origins.

Materials and methods

Hatchery-reared red sea bream used were zero-age juveniles from Kochi Prefectural Fisheries Experimental Station and were kept in the pen-net cages until the experiments started on 23rd, July 1992. Sample size and total length (Mean ± SD) of the juveniles were 300 and 79.08 ± 8.07 mm, respectively. Wild fish were captured on 1st, July 1992 by the dragnet off Fukuma Town in Fukuoka Pref., Kyushu and the experiments were conducted from 8th to 11th, July at the Fisheries Experimental Station of Kyushu University. They were kept in a concrete 2000-l circular tank without feeding from 1st, July to the beginning of the experiment. Sample size and total length were 180 and 62.25 ± 5.80 mm, respectively. Yellowtail, *Seriola quinqueradiata,* (ca 18-21 cm FL) which were being kept in the tanks of the laboratory of fish nutrition, were used as predators.

The experimental procedure of each set was as follows. After netting 30 fish which had no experience of predation pressure (naive) out of the pen-net cage, they were calmly placed in a 20-l tank with weak aeration for 30 min. Then, they were released into an experimental 1000-l tank with 2 yellowtails. A video record of the behaviour of *P. major* (naive group) and *S. quinqueradiata* was made during the 5 min just after release. After predation pressure for 5 min, the survivors were netted and rested in the 20-l tank for 0.5, 1, 3, or 24 hr. In the case of experimental sets on the wild fish, the resting time was always 0.5 hr. After these resting durations, the survivors were released again into a distinct tank and the behaviours of the experienced group and another two yellowtails were recorded, also for 5 min by the video. The video tapes were analyzed every 30 sec for 5 min (300 sec: n=300/30=10 in Table 1) to count the numbers of red sea bream showing the tilting behaviour, preyed on by yellowtail, and attacking behaviour of the yellowtail toward red sea bream. Therefore, when comparing the data on naive and exprienced groups, we adopted a mean of 10 values in each group. In the present study, the term 'learning' refers to a change in behaviour with experience (Dill, 1983).

Eight and six experimental sets were performed for the reared and wild fish, respectively. Two 1000-l blue-coloured circular tanks were used in each experimental set. Releases were conducted twice (naive and experienced groups) into each tank. Thirty juvenile red sea bream and 2 yellowtails were used during each experimental set. For the selection of tilting and non-tilting fish, we used 20-l tank to confirm the presence of their tilting behaviour in the W-Exps. 5 (tilting group) and 6 (non-tilting group). Yellowtails used for the experiments were fed live red sea bream, but not fed 24 hr prior to the predation pressure experiment. Control experiments were also conducted twice for hatchery-reared fish to examine whether or not handling-induced stress affected the behaviours.

Table 1. Percentage of tilting fish of hatchery-reared seedlings in naive and experienced groups (Mean ± SD) in 5 min.

	naive (1st release) (n=30)	experienced (2nd release) (n=30)	resting time (hr)
R-Cont. 1	13.0± 9.2	35.0±20.6 **	0.5
R-Cont. 2	24.0±16.6	30.3±26.5	0.5
R-Exp. 1	37.0± 6.4	34.0± 3.4	0.5
R-Exp. 2	10.0± 6.8	16.7± 3.8 *	0.5
R-Exp. 3	23.0± 9.1	56.9± 6.3 ***	0.5
R-Exp. 4	59.3±11.3	74.3±19.4	1
R-Exp. 5	31.0± 7.7	62.5± 8.1 ***	3
R-Exp. 6	25.0± 8.8	73.8± 5.7 ***	3
R-Exp. 7	50.3±11.9	58.6± 9.3	24
R-Exp. 8	60.0± 6.3	25.3± 5.5 ***	24
Mean±SD (R-Exps. 1-8)	37.0±18.2	50.3±22.1	

* $p<0.05$, ** $p<0.01$, *** $p<0.001$, Mann-Whitney's U test

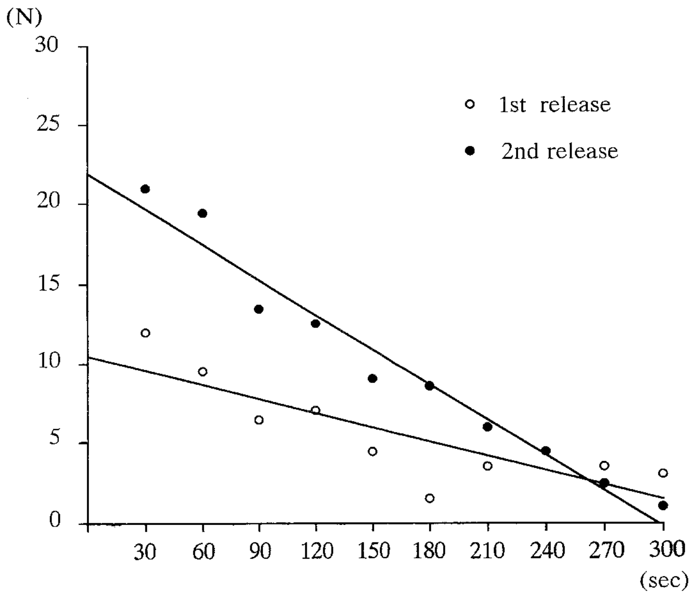

Fig. 1. Changes in mean number of tilting fish in 1st and 2nd releases during 300 sec of two sets (R-Conts. 1 and 2) of the control experiment without predation pressure.

Results

Hatchery-reared fish

Control experiment

Two sets of the control experiment without using predators were conducted to examine the effect of the handling procedure on the tilting behaviour. In these experiments, the resting time between first and second releases was 0.5 hr. The number of tilting fish in the second release was larger than that in the first one in the two experimental sets (Table 1). Furthermore, the difference in the tilting fish number between naive and predation experienced groups was statistically significant in the experiment of R-Cont. 1 (Table 1) (Mann-Whitney's U test, $p<0.01$).

The number of tilting fish in every 30 sec during 5 min (300 sec: $n=10$) decreased with time elapsing in both the first and second releases (Fig. 1). In the first 30 sec, the number of tilting fish observed was largest and the mean numbers of the first and second releases were 12 and 21, respectively. The number of tilting fish observed in the last 30 sec of the experiment was small and the mean numbers in the first and second releases were 3 and 1, respectively. The relation between mean number of tilting fish and time elapsed in the two releases was in the following negative correlations; 1st, $Y=10.433\text{-}0.030X$, $r=0.694$; 2nd, $Y=21.933\text{-}0.074X$, $r=0.965$ (Fig. 1).

Resting time

Eight sets of predation pressure experiment adopting 4 different resting times were conducted to make clear how long the learning effect of predation pressure on the tilting behaviour is retained (Table 1). We compared mean numbers of the tilting fish in every 30 sec during 5 min (300 sec: $n=10$) of the naive group with that of the experienced group in each set. In six sets out of the eight, the mean number of tilting fishes in the experienced group was larger than that of the naive group, and in four sets (two of 0.5 and 3 hr each) of the six the difference between the two groups was statistically significant (Mann-Whitney's U test, Table 1). The difference between them was largest at the rest time of 3 hr (Table 1). By contrast, the mean value of the naive group in R-Exp. 8 was significantly larger than that of the experienced group at the rest time of 24 hr.

Predation pressure experiment

We excluded two sets at the rest time of 24 hr (R-Exps.7 and 8) from this section because of the uncertainty of predation pressure effect on the tilting behaviour and adopted six sets (R-Exps. 1-6) (Table 1). Total mean values of the tilting fish for the naive and experienced groups in the six sets were 30.9% and 49.9%, respectively. This difference in mean rate between these groups was statistically significant (Mann-Whitney's U test, $p<0.001$). The rate of tilting fish increased about 20% after experiencing predation pressure.

When analyzing mean rates of every 30 sec in 5 min through six sets distinguishing naive ($n=6$) and experienced ($n=6$) groups, it was found that the naive group showed no marked fluctuations of the mean rate of about 23%. By contrast, the experienced group seems to show a gradual increasing trend from 37.1% to 52.1% with time elapsing (Fig. 2). A positive correlation could be given with the relation between tilting fish rate and time elapsed; $Y=39.740+0.047X$, $r=0.803$, suggesting that tilting fish numbers in the experienced group increase with time.

Attack and predation against swimming and tilting fish

From the video tape, we counted separately the number of attacks by the yellowtails against swimming and tilting fish and calculated the number per each individual for 5 min in the six sets. The number of attacks was larger for swimming fish than for tilting fish ; naive fish, 6.5 times and experienced fish, 8.7 times larger, and the differences were statistically significant (Mann-Whitney's U test, $n=6$ (six sets), $p<0.01$) (Table 2). This shows that the swimming fish are more easily targeted as prey than the tilting fish. Comparing the values of the naive fish with those of the experienced fish, those of the latter were larger than the former except one case of tilting group of R-Exp. 5. This means that the swimming fish in the experienced

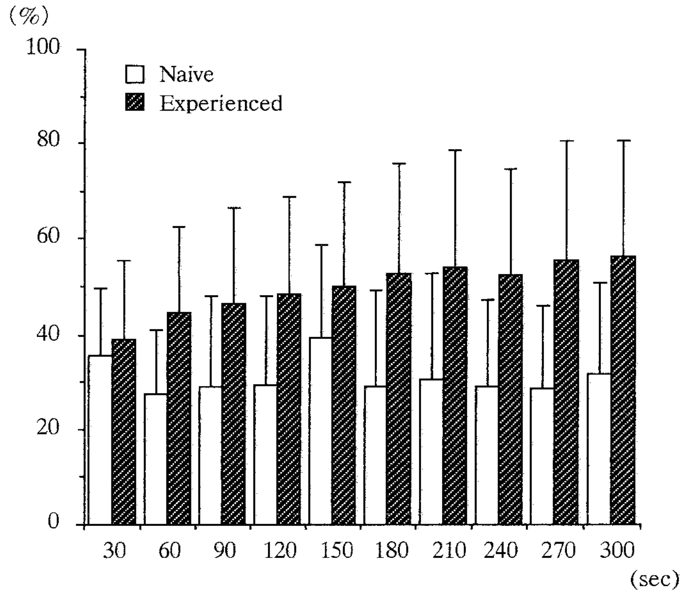

Fig. 2. Rates (Mean ± SD) of tilting fish in naive and experienced groups of hatchery-reared juveniles used in R-Exps. 1-6 during 300 sec.

Table 2. Frequency attacked and predation rate of hatchery-reared juveniles in R-Exps. 1-6 of Table 1.

	Attacked No. per each fish in 5 min (mean ± SD)		Predation rate (%) (Mean ± SD)	
	swimming	tilting	swimming (N)	tilting (N)
naive	2.6±1.4	0.4±0.3 **	1.9±2.4(6)	11.7±11.2(3)
experienced	5.2±2.8	0.6±0.5 **	0.3±0.8(1)	20.4±39.3(4) *

(N): No. of fish preyed on. * $p<0.05$, ** $p<0.01$, Mann-Whitney's U test.

group tend to be attacked more concentratedly.

Liability to being preyed upon (predation rate: PR) was examined in swimming and tilting fish of the six experimental series on the basis of numbers attacked (AN) and numbers preyed on (PN) (Table 2). PR is given by the following equation;

$$PR = (PN / AN) \times 100$$

Table 2 shows that the predation rate is larger in the tilting fish than the swimming fish in both naive and experienced groups, and especially in the experienced group the difference between swimming and tilting fish is statistically significant (Mann-Whitney's U test, $n=6$, $p<0.05$).

We divided an experimental period of 5 min into the first 10 sec and the remaining 290 sec to analyze when yellowtail preyed on red sea bream. Table 3 shows that during the 10 sec just after release, 43 % (3/7) of the swimming fish preyed upon were captured. No tilting fish were preyed upon during the first 10 sec and all tilting fish preyed upon were captured after the disorder caused by the release.

Table 3. Time of predation occurred on swimming and tilting hatchery-reared juveniles in R-Exps. 1-6, distinguishing 10 sec just afte release from remaining 290 sec in 5 min.

	percentage of fish preyed on (N)	
	0~10 sec	10~300 sec
swimming	21.4(3)	28.6(4)
tilting	0 (0)	50.0(7)

(N): No. of fish preyed on.

Table 4. Number of tilting fish of wild juveniles in naive and experienced groups (Mean ± SD) in 5 min.

	naive (n=10)	experienced (n=10)
W-Exp. 1	0.1±0.3	0.7±0.5 *
W-Exp. 2	0.0	0.3±0.5
W-Exp. 3	0.0	0.2±0.6
W-Exp. 4	0.0	0.0
W-Exp. 5	0.0	0.0
W-Exp. 6	0.5±0.2	2.6±2.6
mean±SD	0.1±0.2	0.6±1.0

* $p<0.05$, Mann-Whitney's U test.

Wild fish

Predation pressure experiment

When released into a tank containing two yellowtails, most individuals of the red sea bream did not tilt, but fled away almost in order forming a school from the predators both in naive and experienced groups. No significant differences could be found in numbers of the tilting fish between naive and experienced groups in six experimental sets except W-Exp. 1 (Table 4). The mean number of fish that tilted in the naive and experienced groups was 0.1 and 0.6, respectively, though they were attacked by the predators. Tilting fish tended to appear and increase in number at the latter half of the 5 min (Fig. 3).

In the present study, wild juveniles of red sea bream were weak in showing tilting behaviour under the predation pressure. However, tilting fish could be observed in the handling procedure process. Thirty individuals showing tilting behaviour were selected and put under the predation pressure (W-Exp. 5). During that,

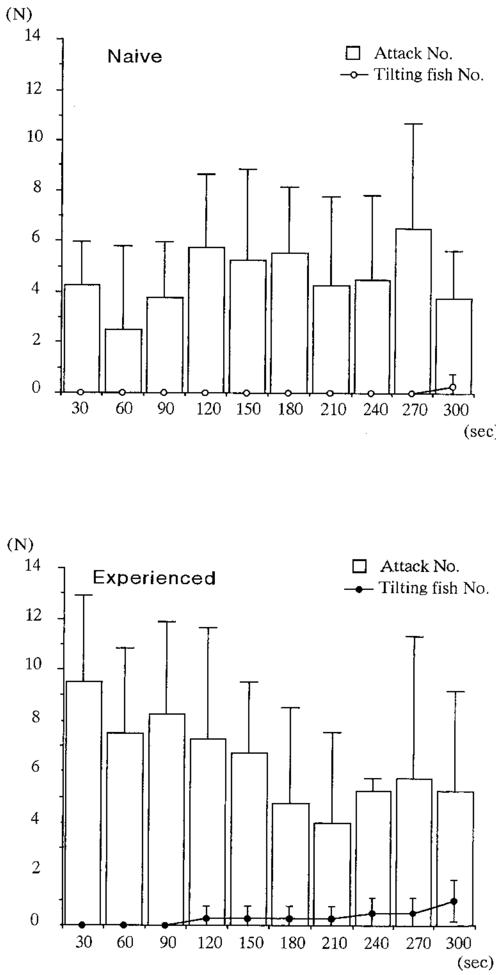

Fig. 3. Number (Mean ± SD) of fish tilted and of attacks in naive and experienced groups of wild juveniles used in W-Exps. 1-4 during 300 sec.

they did not tilt at all and all individuals swam away from the predators, though they tilted without predation pressure just 30 min before the release. Another thirty individuals not showing tilting behaviour were also selected and used for the experiment (W-Exp. 6). Contrary to the expectations, they showed the maximum value of the tilting fish number among the six sets (Table 4).

Discussion

A preliminary study by Yamaoka *et al.* (1991) reported that hatchery-reared juveniles of *P. major* have an ability to learn the tilting behaviour under predation pressure by the young of S. *quinqueradiata*. However, as criticized by Uchida *et al.* (1993), they did not conduct the control experiment without predators and, therefore, the possibility remained that the increase in number of the tilting fish after experiencing predation pressure was due to the effect of handling-induced stress. In the present study, hatchery-reared juveniles showed the tilting behaviour without predators and more tilting fish appeared in the second release (experienced) than in the first release (naive). However, the number of tilting fish decreased quickly without predation pressure, especially in the second release (Fig. 1). The effect of handling on fish behaviour, which is conspicuous just after the releases, can be considered to become almost extinct in 5 min. By contrast, in the experiments with predation pressure the number of artificial fish showing tilting behaviour did not decrease with time but increased in the experienced group (Fig. 2). This suggests that the predation pressure by yellowtail might be learned by the red sea bream juveniles and, as a result, the number of tilting fish increased in the experienced group. The liability to tilting in juveniles of red sea bream can be reinforced by experiencing predation pressure put on by yellowtail. Tsukamoto (1990, 1993) and Uchida *et al.* (1993) supposed that a liability degree of individuals toward tilting varies and is something like an individuality.

The ability of hatchery-reared juveniles in salmonid species to learn predation pressure was studied by many authors. Kanid'yev *et al.* (1970) reported that experienced fish displayed enhanced ability to avoid predation and hatchery-reared fish could be trained to recognize predators in advance of releasing into natural waters. Ginetz and Larkin (1976), Patten (1977) and Olla and Davis (1988, 1989) suggested that hatchery-reared juveniles of the genus *Oncorhynchus* could learn the predation pressure and survival rates of the conditioned fish became higher than the unconditioned fish. Goodey and Liley (1986) also found that guppies (*Poecilia reticulata*) that have experiences being chased in the early ontogenetic stage by adult conspecifics required more attacks before they were preyed on than those exposed to only visual or chemical cues provoking chasing. Recently, Suboski and Templeton (1989) reviewed studies on life skills training for hatchery fish and concluded that many fish species can learn to recognize the stimulus features of food, predators and habitat. Fish that visually observe predators preying on conspecifics later show enhanced ability to evade such predators. They suggest that large scale training of predator recognition may be effective before hatchery fish are released to the wild. It is apparent that learning plays an important role in the life of fishes in their responses to environmental changes (Kieffer and Colgan, 1992).

In the present study, it was made clear that the tilting behaviour functions as a means to hinder the motivation of prey targeted by yellowtail (Table 2). This tendency is especially conspicuous during 10 sec just after the release and, at that time, the frequency of fatal attacks toward swimming fish was markedly higher than toward tilting fish (Table 3). Contrary to the case of attacks by yellowtail, the predation rate was higher in tilting fish than in swimming fish, which suggests that the tilting fish are hard to be targeted as preys by yellowtail, but once they are targeted they are easily preyed on. This fact might occur because the tilting fish are exposed to predators in the tank for 5 min and during that time the predator's eyes grow accustomed to the tilting behaviour.

Using drag-net data, Uchida *et al.* (1993) examined the difference in survival rates between tilting and non-tilting juveniles of hatchery-reared red sea bream by releasing them together into natural environments. They showed that a larger number of tilting fish released were captured than non-tilting fish. Two reasons can be suggested for this fact. One is really the higher survival rate of the tilting fish, and the second reason is that the tilting fish have a tendency of being stationary near the release point and do not disperse widely. In either case, these features seem to be advantageous to the stocking program. The tilting behaviour might function as a predator avoidance tactics in natural environments, though a definite mechanism is unknown.

Predator-avoidance behaviours might differ between hatchery-reared and wild juveniles in red sea bream. When put under the predation pressure, many hatchery-reared fish exhibited the tilting behaviour (Fig. 2). Howerver, the number of wild juvenile tilting fish was very small or none and the predation pressure could not affect the change of fish behaviours (Fig. 3). Furthermore, wild juveniles from off Kyoto Pref. at about one day after capture did not tilt without predation pressure in a 500-l tank (Yamamoto and Yamaoka, unpublished). However, Tsumura and Yamamoto (1993) and Uchida *et al.* (1993) reported that wild juveniles sampled from Setonaikai Inland Sea and News Bay in Ohita Pref., respectively have a strong tendency toward tilting behaviour in the predator free condition. Tsumura and Yamamoto (1993) supposed the density of fish to affect the tilting behaviour when put in an artificial new environment and inferred that the higher the density they were kept, the weaker the tilting behaviour.

This result is opposed to that of the present study. One reason for this difference is due to the lack of predators in the experimental series of Tsumura & Yamamoto (1993) and Uchida *et al.* (1993). Another reason might originate from the different duration of time between capture and start of the experiment. In Tsumura & Yamamoto (1993) the duration is shorter than 24 hr and it is about a week in the present study. It is probable that behavioural characteristics which had been gained in the natural habitat vanished and newly acquired, hatchery-reared ones were revealed after being kept in a 2000-l circular tank for a week. However, we cannot help denying the possibility of, at least, density effect, because in the present study the wild fish density in the 2000-l circular tank of the Kyushu University and that of their low-density experimental set (100 fish/1000-l) [*1] is similar and, according to the suggestion by Tsumura & Yamamoto (1993), wild juveniles off Fukuoka Pref. should have shown strong tilting behaviour like low-density hatchery-reared fish. Yamamoto *et al.* [*2] also suggested that fish in the starved condition were weak in showing the tilting behaviour. Since wild fish used in the present study were reared without feeding for a weak before experiments, they could be in the starved condition. The possibility exists that the starvation weakened the tilting behaviour of wild fish. However, during handling procedure many tilting fish could be observed. Therefore, we cannot consider that only the starvation crucially affected the tilting behaviour in this case. These facts suggest that artificial and wild juveniles of this species seem be considered to adopt different tactics under predation pressures. Wild juveniles must have survived the risk of predation and those experiences might affect the behaviour for predator avoidance.

Uchida *et al.* (1993) regarded the tilting behaviour as a fear response to frightening stimuli

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[*1] Y. Yamamoto, pers. comm.

[*2] Y. Yamamoto, S. Tsumura, A. Matsumoto, S. Imamura and H. Nakano: Summary of oral presentation at the annual meeting of Nippon Suisan Gakkai, in Tokyo, 1992, p. 101.

and supposed that wild juveniles which showed stronger tendency toward the tilting behaviour than hatchery-reared ones were more sensitive to the stimuli. Following their supposition, the wild juveniles used in the present study can be regarded non-sensitive to the stimuli. However, since they showed the tiling behaviour during handling procedure without predation pressure in the 20-l tank, they can be sensitive enough to show the behaviour. Small size of the tank used in the experiments also seems to be a factor affecting the behaviour. The size of the tank used by Uchida *et al.* (1993) was 70-l, smaller than that used in the present experments, 1000-l. The fact that no tilting behaviour was observed when released into natural environments[10] might be related with the size of the place where released. Therefore, it could be concluded, at least so far, that some ecological factors including density of conspecifcs, presence of predators, career on an exposure to predation and the size of tanks may affect the tilting behaviour of juvenile red sea bream. That is, the threshold of the tilting behaviour seems to be variable according as environmental factors.

To understand the biological meaning of the tilting behaviour and its flexibility, as suggested by Kieffer & Colgan (1992), comparisons of natural fish populations that are influenced by different selection pressure acting upon them will be important. We also think it important to examine the tilting behaviour in closely related species, for example, crimson sea bream and black sea bream, to infer the function of the behaviour.

Meanwhile, the tilting behaviour can also be grasped from the viewpoint that it is a response to the predation stress. Hereafter, the tilting behaviour needs to be studied as a behavioural indicator of the stress or in relation to other behavioural features such as the territorial behaviour found in the juvenile red sea bream (Yamaoka et al, 1991, 1992; Yamada et al., 1992; Mori et al., 1993).

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