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Effects of high food-demand fish removal in groups of juvenile sea bass (*Dicentrarchus labrax*)

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Abstract: In self-feeding conditions, a few individual sea bass (Dicentrarchus labrax (L., 1758)) display strong activity in striking the food dispenser, whereas the remaining individuals of the group actuate the feeder weakly or never. Here, we investigated the effects of removal of the individuals showing dominant activity on the social and feeding behaviours in groups of juvenile sea bass. Following removal, new fish showing a dominant self-feeding activity quickly appear. They always come from the group of fish that have a low number of triggering actuations. This observation shows that it takes less time, about 5 days after the removal of dominant triggerers vs. 14 days at the beginning, for the re-establishment of the behavioural structure, suggesting the possibility of social transmission between individuals. The fish that show weak triggering activity seem to reach the high-food triggering level without obvious signs of competition. This experiment reveals the importance of the food-demand behavioural structure: the fish displaying the highest activity lead to a general food distribution and play a dominant role in feeding the entire group. Functional plasticity in this role within individuals is also demonstrated, indicating that the high-triggering function is essential for the group and not for the individual themselves.

Résumé : Au sein d'un groupe de bars (*Dicentrarchus labrax* (L., 1758)) placés en auto-nourrissage, quelques individus disposent d'une activité forte de déclenchement volontaire du distributeur d'aliments. Les autres poissons du groupe disposent d'une activité de demande faible voire nulle. Ici, nous avons étudié l'impact du retrait des poissons à forte activité sur le comportement alimentaire et social de groupes de bars juvéniles. De nouveaux individus à forte activité réapparaissent rapidement, provenant exclusivement de la classe de poissons de faible demande. Cinq jours en moyenne suffisent après le retrait, contre 14 jours au début de l'expérience, pour que la structure comportementale se rétablisse suggérant l'existence d'une transmission sociale entre les individus. Ces poissons de faible activité semblent de plus atteindre leur nouvelle fonction sans aucun signe de compétition. Cette expérience révèle d'abord l'importance de la structure de la demande alimentaire puisqu'elle réapparaît après le retrait. Elle montre également que l'activité des forts manipulateurs conduit à une distribution générale de l'aliment et contribue à nourrir le groupe en entier. L'étude montre enfin une plasticité fonctionnelle indiquant que seule la fonction de manipulateur fort est essentiel pour la stabilité du groupe, non l'identité des individus par elle-même.

Introduction

In the wild, the social structure of fish can extend from a solitary and territorial lifestyle to a schooling behaviour sometimes composed of thousands of fish (Pitcher and Parrish 1993; Grant 1997; Hoare et al. 2000; Hoare and Krause 2003). These behavioural differences are determined by the type of habitat where fish live and by environmental factors such as the distribution and the availability of resources (Grant 1997). In extensive rearing systems such as in cages or in net-pens where the densities of fish are high, the social structures are not so different from that in the wild. Observations show that some fish form small schools while others are more solitary within the group. However, due to the extreme difficulty to observe social behaviour of farmed fish in high density environments, most studies were done at lower densities in experimental tanks, i.e. one or several tens of individuals per cubic meter, whereas fish farms generally have much higher densities of fish, i.e. thousands of fish per cubic meter. In such experimental conditions, a dominance hierarchy for feeding often occurs in salmonids such as in Arctic char *Salvelinus alpinus* (Brännas and Alanärä 1993; Alanärä et al. 1998). However, the space restriction leads some fish species to adopt a synchronized schooling behaviour as the best and the least costly social strategy for them. Anyway, the group structure of fish may be influenced by routine farming procedures such as handling and sampling, or just by death of some fish, which may result in behavioural disturbances. The impact of such removal on the behaviour of the remaining group members depends firstly, on the social structure characterizing each gregarious species, and secondly, on the social role of the moving individual in the group (Lazaro-Perea et al. 2000; Lemasson et al. 2005).

We present here an experimental study which focused on the social structure of European sea bass juveniles *Dicentrarchus labrax* L. (1758) held in groups under self-feeding system. In nature, European sea bass forage in schools, sometimes consisted of several thousands of individuals, when they are juveniles (Barnabé 1980; Bégout Anras et al. 1997). Moreover, previous experiments have demonstrated the schooling character of sea bass in captivity, showing marked behavioural disturbance in conditions of isolation (Anthouard 1987). This species is also able to learn to use a self-feeder device by biting on a trigger to obtain food and self regulate the food supply. This ability offers the opportunity to carry out an experimental study about the voluntary food-demand behaviour and the social relationships within a group during foraging behaviour. The development of techniques such as the computerized on-demand feeding system coupled with a PIT-tag monitoring device have successfully contributed to show inter-individual differences in the triggering response of juvenile sea bass, estimated by the individuals' feed-triggering activity level (Covès et al. 2006; Di-Poi et al. 2007; Millot et al. 2008). A population of 50 individuals was always composed of only a few "leader" individuals that displayed a dominant triggering activity, some fish that showing a low-triggering activity and the remaining individuals, the "inactive", that had a zero-triggering activity on the feeder.

In the present study, we tested the impact of the removal of the "leaders" within juvenile sea bass groups. We observed the changes in food-demand and social behaviours following this removal at short term (25 days after the removal), and compared this to the pre-removal situation (42 days before removal). In this way, an emphasis was put on the learning time of the self-feeder used before and after the removal.

Material and methods

Experimental fish and rearing conditions

The experiment was conducted at Ifremer Experimental Station in Palavas (France) with 300 juvenile European sea bass *Dicentrarchus labrax*, hatched and grown at a fish farm

(EXTRAMER, Salses, France) and randomly divided into six groups of fifty individuals (tanks no. 1, 2, 3, 4, 5 and 6). The initial average weights of fish ranged from 279 to 295 g. Each sea bass group was stocked in 1 m^3 tanks (size: 1×1×1 m) that were supplied with sand filtered and UV-treated seawater (salinity: 38, pH: 8) in a flow-through system (flow rate: 1 $m^3.h^{-1}$). Water temperature was maintained at 21.0 ± 1.0 °C and oxygen concentration above 80% saturation in the outlet. Tanks were illuminated with 75 W lamps placed 70 cm above the water surface. Photoperiod was 16:8 LD (400 Lux: total darkness, light onset at 06:00 UT) with twilight transition periods of 30 minutes. Fish were fed a commercial sea bass diet (SICA Le Gouessant®-Grower Extrude Natura, Lamballe, France). Food pellets were composed of 44% crude protein and 22% lipid and were approximately 4-5 mm in diameter. Feed hoppers were daily filled and uneaten pellets were counted in the sediment trap during the standardised animal care procedure performed from 10:00 UT to 11:00 UT.

Experimental apparatus

Before the experiment, all fish were anesthetized in a 0.08‰ eugenol bath. In a few seconds, a Passive Integrated Transponder “PIT-tag” (Micro-BE, Toulon, France) including an identification code was implanted horizontally in muscles, just behind the skull, with a sterile implanter (plastic syringe with a 23 mm x 2.63 mm needle) into each fish. The small size of PIT-tags (SarWin, 12.23 mm x 2.06 mm; 0.05 g) eliminates negative impacts on fish with little or no influence on growth-rate, behaviour and health (Prentice et al. 1990; Quartararo and Bell 1992; Baras et al. 1999, 2000; Gries and Letcher 2002; Navarro et al. 2006). In our study, no observation of behavioural changes and no alteration of fish growth and health were noted. Each tank was equipped with one self-feeder (Imetronic, France) that included a food dispenser, a sensor and a control box connected to a computer (Covès et al. 1998; Rubio et al. 2004; Fig. 1). The sensor consisted of a metal trigger protected by a PVC pipe placed in a forward position and surrounded by the PIT-tag detection antenna (Micro-BE, France) (Covès et al. 2006). Thus, fish had to enter through the PVC pipe where the PIT-tag was detected by the antenna, and then, the trigger was actuated. The software employed was designed to register identification codes that correspond to a hit on the sensor. At every actuation, the PIT-tag detection and food distribution were counted and stored in a computer file. At each actuation, the food dispenser distributed 22 to 28 pellets (mean weight: 123.5 mg/pellet) from the beginning to the end of the experiment, corresponding to a constant reward during the experiment of 0.5 g per kg of fish. Food dispenser was placed 30 cm far from the trigger location whereas food pellets were delivered around 15 cm far from the trigger area.

To verify the reliability and accuracy of the monitoring system: 100% of identification codes were recognized at least once in all experiments. Furthermore, approximately 96% on average of the total number of registered actuations were paired with corresponding identification code registrations.

Protocol of the removal experiment

The experiment was designed to determine the impact of removing identified fish, showing dominant activity on the feeder, on food-demand and social behaviours, i.e. agonistic and territoriality, of the remaining individuals in each group. The experiment extended over a 68-day period which is the necessary time to observe a stable behavioural structure in the fish groups (Covès et al. 2006; Di-Poi et al. 2007). Three tanks were designated as “removal” tanks (tanks 1, 4 and 5) where the fish displaying a dominant activity were removed at day 43. The three remaining tanks (tanks 2, 3 and 6) were used as “control” tanks in which any fish were removed at day 43. Control tanks allowed us to evaluate the temporal stability of the group structure over the course of the 68 day trial. In both removal and control tanks, behavioural observations were made and compared over the two phases before and after the removal at day 43: Period 1 (day 1-42) and Period 2 (day 44-68).

Food behaviour monitoring

Before the experiment, fish were allowed two weeks to adjust to their new experimental environment and become familiar with the triggering system. Experimentation took place over 68 days during which two variables were monitored:

- the individual food-demand behaviour estimated by the individuals’ feeder triggering activity level: this was calculated using the proportional contribution of each fish to the total number of trigger actuations of the group in each tank. Differences in food-demand level and in regularity of triggering activity during the experimental period were distinguished between high-triggering fish group showing the dominant activity on the feeder (> 15% actuations distributed regularly as at least one actuation in mean per day), low-triggering fish group (< 15% actuations distributed as less than one actuation in mean per day) and zero-triggering fish group (zero or one actuation during the experiment). It was assumed that the single actuation of the zero-triggering individuals were involuntary.
- the total food intake: the uneaten pellets in the sediment trap were counted daily. Then the complete number of pellets dispensed by the feeder minus the whole number of uneaten pellets was calculated to determine the total amount of food intake by all fish in each tank.
- the learning phase was a no triggering period defined as the time elapsed prior to the first actuation of a high-triggering fish. It was recorded before and after the removal: Period 1 “before removal” defined as day X minus day 1, and Period 2 “after removal” defined as day X minus day 44.

Agonistic interactions and territorial behaviour

Video recordings of the six tanks were taken during three defined periods: day 15 to 20, day 30 to 35 and day 44 to 50 using an analogical system including CCD cameras (Panasonic WV BL 200) and S-VHS recorders (Panasonic AG 6010). 329 video sequences corresponding to 329 trigger actuations in control tanks were also analysed and were divided into 278 trigger actuations from high-triggering fish and 51 trigger actuations from low-triggering fish. In removal tanks, a total of 200 video sequences were analysed before day 43 demonstrating 134 actuations of the trigger from high-triggering fish and 66 actuations from low-triggering fish. After the removal, 114 actuations from new high-triggering fish and 50 actuations from low-triggering fish were analysed.

Observations were made in an effort to determine whether the fish that actuated the trigger:

- had preferential access to the feeding area: time spent by the triggering fish close to the trigger and within the area where food pellets were delivered;
- occupied a larger territory than the others: observation of the group repartition;
- was aggressive towards his congeners to defend his territory and the food resources, i.e. trigger and pellets delivered. The number of intimidation acts, i.e. fast movement of a fish towards another without physical contact, and severe attacks ending with bites were quantified. The video tracking was followed by the inspection of the fish bodies at the end of the experiment. The presence of marks of attacks, fins scars or wounds was counted.

Finally, we compared the agonistic and territorial behaviours before and after the removal of the high-triggering animals within each removal tank.

Growth

Each fish was weighed at the beginning and at the end of the experiment. The individual specific growth rates (SGR) were calculated as: SGR = $[(\ln W_f - \ln W_i) / t] \times 100$ in %, where

W_i and W_f are respectively the initial and final body weight (in g) and t, the number of days between measurements (42 or 68 days according to the fish tank).

Data analysis

Data analyses were performed with StatView 5.0 (SAS Institute Inc.). The results were expressed as means ± standard error (SE). Durations taken prior to first actuation by high-triggering fish before and after the removal were compared using a Student's *t*-test. A one-way analysis of variance (ANOVA) was used to test differences in initial weights between the three triggering groups (high-, low- and zero-triggering activity) for each tank. We ran similar analyses on the final weight and the specific growth rates. $P < 0.05$ was taken as the statistically significant threshold.

Ethical note

The experimental protocol was approved by the Jean Monnet University's Animal Care Committee and by the IFREMER Institute (agreement no. A-34-192-6).

Results

In control tanks

Food-demand behaviour

Over the period 1 (day 1 to 42), the individual food-demand behaviour of fish was observed within each tank to determine group classification (Fig. 2 and Table 1). In each tank, 4 to 5 individuals displayed a high number of triggering (72 to 79%), they were the high-triggering fish. An average number of 24 low-triggering fish (from 23 to 25 individuals) shared from 19 to 26% of the total actuation number. The remaining individuals were the zero-triggering fish (21 in mean) and triggered less than 2% of the total actuation events. During period 2 (day 44 to 68), the groups remained in a similar structure with average values of 4 to 5 high-triggering fish, 17 low-triggering fish and 28 zero-triggering individuals. No uneaten pellets were counted in the sediment trap in the three tanks over the experiment. Then, the amount of food delivered per day was equivalent to the amount of food eaten per day by the population (Table 1). In each tank, the average quantity of food delivered and intake per day increased from period 1 to period 2 (mean ± SE = 76.8 ± 8.3 g of food/day on period 1 vs. 110.9 ± 7.5 g of food/day on period 2; Table 1).

Individual plasticity

The 4 to 5 fish classified as high-triggering fish in the control tanks were not always the same individuals throughout the experiment (Fig. 2 and Table 2). 3 individuals on the 4 or 5 high-triggering fish according to the tanks displayed regular high food-demand behaviour during the course of the 68-day experiment; whereas others demonstrated this pattern only at the beginning (period 1) or at the end (period 2) of the experiment. 1 or 2 fish on the 4 to 5 high-triggering fish were high-triggering individuals during specific times and then, they switched their activity status to become low-triggering individuals at the end of the experiment. Conversely, the same number (1 to 2 individuals) of low- or zero-triggering individuals changed their activity behaviour to become high-triggering animals. Despite the individual switches, the number of high-triggering fish remained unchanged during the two periods.

Agonistic and territorial behaviours

Outside of the feeding period, the recordings did not show differential use of space occupation between fish. The high-triggering fish did not spend time close to the trigger location or in the food delivery area. Generally, all the fish gently swam in a disorganized way in all directions, even if according to the tank, they adopted a homogeneous swimming in school all around the pond. During the feeding period, the high-triggering fish left the group in the direction of the trigger to actuate the feeder. Sometimes, a sub-group of 4-5 fish gathered in crown in front of the trigger area can be observed during an actuation. Just after, the high-triggering fish quickly joined the grouping already waiting for food in the feeding area. During waiting, the grouping seemed agitated and showed disorganized swimming. A few seconds after the actuation (3-4 s), the food pellets were delivered in the water. The fish enhanced their agitation until all the pellets were eaten. If a kind of competition can be observed during the food delivery, there was no competition for the trigger itself. The high-triggering fish did not show strong territory defence behaviour. They did not exhibit aggressive acts to prevent the other fish from having access to the trigger or to the feeding area. Moreover, the absence of scars or marks on the 150 fish bodies showed that no severe competition occurred during the feeding phase. After feeding, all the fish including the high-triggering fish, left the food delivery zone without coherence in their trajectories. After a few minutes, the fish went back to their initial swimming behaviour and did not care both to the trigger and to the feeding area until the next feeding time.

In removal tanks

Food-demand behaviour

Period 1*:* 3 to 4 high-triggering individuals were responsible for 70 to 83% of the total food-demand (Fig. 3 and Table 3). Approximately 22 low-triggering fish (from 16 to 27) handled the self-feeder, corresponding to 23% of the total food-demand. The 25 remaining fish were zero-triggering individuals and shared less than 3% of the total food-demand activity. During this period, no uneaten pellets were counted in the three assay tanks.

Period 2*:* After the removal, a similar structure to the one of period 1 was observed (Fig. 3 and Table 3). Specifically, 3 to 4 fish were high-triggering fish and their activity corresponded to 78% on average of the total food-demand. An average of 17 low-triggering fish shared between 8 to 25% of total number of actuations while the remaining 25 individuals were categorized in the null food-demand group, triggering less than 2% of the total food-demand activity. The removal of the high-triggering fish did not have effect on the food wastage. No uneaten pellets were counted in the tanks after the removal. As in control tanks, the average quantity of food delivered and eaten per day increased between the pre- and the post-removal periods in each tank (mean ± SE = 62.3 ± 3.2 g of food/day on period 1 vs. 88.6 ± 7.2 g of food/day on period 2; Table 3).

Remaining group structure and individual plasticity

Following the removal of the high-triggering fish, the behavioural structure was reformed with new individuals showing a dominant food-demand activity (Fig. 3). More specifically, approximately 90% of these new high-triggering fish were low-triggering individuals before the removal. However, the number of high-triggering fish remained unchanged before and after the removal within each tank (Table 3). The switch from low to high-triggering activity for some fish underlines the functional individual plasticity in food-demand behaviour.

Agonistic and territorial behaviours

Period 1: There were no behavioural differences observed between the control and the assay tanks over the period 1. As previously described, there was no differential space occupation, no competition for the trigger location or the food area access and no marks of aggression on the fish bodies.

Period 2: The removal did appear to disturb neither the feeding behaviour nor the social interactions of the remaining fish. No excitement or other stress responses were observed within the remaining group. Moreover, the presence of a new high-triggering fish seemed to be accomplished without competition. No aggressive behaviour and no attempts of intimidation were noted on the video recordings neither for the access to the trigger nor for the access to the food delivery area. It was confirmed by the absence of marks on the fish bodies.

Learning phase

For the three assay tanks, the high-triggering fish were observed to actuate the trigger for the first time 14 days in average after the beginning of the experiment, whereas the new high-triggering fish actuated the trigger for the first time only five days after the removal (Table 4). This second "learning phase" was significantly lower than the first one (*t*-test, $t = 4.869$, $P = 0.0082$; Table 4).

Growth

No differences were found in average initial weights (ANOVA, $F_{0.05(5,294)} = 0.497$, $P = 0.778$; Table 5) and in average final weights between tanks (ANOVA, $F_{0.05(2,147)} = 0.543$, $P = 0.582$ for the 42-day tanks; $F_{0.05(2,147)} = 0.484$, $P = 0.618$ for the 68-day tanks; Table 5). There were no significant differences in average initial weights (ANOVA, $F_{0.05(2,46)} = 1.508$, $P = 0.232$;

Table 5) and in average final weights between the three triggering groups of fish in all tanks (ANOVA, $F_{0.05(2,46)} = 0.489$, $P = 0.617$; Table 5). Moreover, the specific growth rates in each tank were not significantly different between the three triggering groups of fish (ANOVA, $P > 0.05$; Table 5).

Discussion

Food-demand behaviour constancy and individual plasticity

As previously described by several authors (Covès et al. 2006; Di-Poi et al. 2007), the present study confirmed that within a group of 50 juvenile sea bass, only a few individuals were responsible for the majority of the group food-demand, whereas the rest of the population exhibited the defined low or zero-triggering activity. This group structure appeared to remain unchanged over the 68-day experiment. Moreover, our results were in agreement with the observations of Covès et al. (2006) and Di-Poi et al. (2007), showing that in such medium-term experiment, the high-triggering fish did not exhibit neither a higher initial and final body weight nor a higher average specific growth rate than the low- and zero-triggering fish. However, a long-term experiment conducted over two thousand days, revealed that these few high-triggering individuals had a transient higher growth during the time they became high-triggering fish in the tank, their specific growth rate increased and was higher than that of the other fish (Millot et al. 2008). In our study, the high-triggering fish did not exhibit benefice in growth suggesting that these fish did not obtain the highest food intake. It may be explained by the absence of obvious sign of dominance behaviour of these individuals towards their congeners both for the access to the trigger and to the resources. The absence of strong aggressive interactions could be due to our population density (50 fish per m^3). Indeed, it is known that fish density has negative consequences on social interactions between individuals (Anthouard et al. 1986; Baker and Ayles 1990; Brown et al. 1992).

During our experiment, the low and zero-triggering fish like the high-triggering fish, exhibited positive growth rates. It means that they had access to the food delivered and that they obtained a sufficient food intake to growth without to be strongly active on the feeder. The video recordings confirmed these results, all the fish were seen to have access to the feeding area during the pellet delivery. Our results also showed that the average quantity of food delivered and eaten per day strongly increased between the beginning and the end of the experiment. It seems to indicate that the high-triggering fish enhanced their number of trigger actuation with the increasing of the food requirements of the growing fish. Firstly, the high-triggering fish seemed to feed the entire group. In addition, feed distribution and thus, high-triggering fish activity, seemed to be adjusted to the group needs (evolving biomass) rather than to the individual’s needs. These conclusions have ever been suggested for sea bass juveniles in similar experimental conditions (Covès et al. 2006; Millot at al. 2008). Moreover, Anthouard (1987) was the first to show that the triggering performance of the only three leaders in a group of 20 juvenile sea bass continued to improve over the experiment, likely reflecting both the improved learning and the increasing nutritional requirements of the maturing fish. Anthouard (1987) concluded that there is a greater trophic activity in sea bass when they are exposed to conspecifics which themselves show heightened feeding activity.

Effect of the removal

Without attempt on the fish group, some individuals altered their triggering activity over the course of the experiment changing from high to low or even low or null to high triggering behaviour. In control tanks, if the high-triggering fish were not necessary the same from the beginning to the end of the experimentation, their number remained also unchanged.

Interestingly, this consistency in behavioural structure was supported by results of the removal tanks, in which the number of high-triggering fish removed was replaced by the same number of new high-triggerers. It appears that it is the high food-demand function of the individual, not the high-triggering individuals themselves, that is essential for the group functioning and perhaps for its stability. The individual plasticity may have facilitated continual group function when the leader of the group structure was removed. Moreover, the removal did not appear to disrupt the group welfare, no weight loss or no food wastage was observed. The food-demand level of the group also did not reduce and the social interactions of the remaining fish were not disturbed. Moreover, the new high-triggering fish seemed to reach the high food status without aggressive competition. They did not show strong territory defence behaviour to prevent the other fish from having access to the trigger or to the feeding area. We also observed that the new high-triggering fish took nine days less to engage in trigger activity than the initial learning period at the beginning of the experiment. This is a significant difference in learning time suggesting that these individuals have ever integrated the functioning of the feeder by observation of the first high-triggering fish. Moreover, the "leaders" seemed to use information from their group to acquaint themselves with the global nutritional requirements. After the removal, the number of trigger actuation of the new high-triggering fish did not reduce; even it was enhanced reflecting probably the increasing of the food needs of fish. These observations confirmed the possibility of social transmission in sea bass juveniles ever suggested by Anthouard (1987). In his study, Anthouard (1987) showed that juvenile sea bass having achieved good performance in a task, i.e. pushing a lever to obtain food, served as demonstrators for conspecifics naive to the task, who themselves were able latter to engage in the same operant act only through visual observations.

The social model underlying the differences in food-demand behaviour

The social pattern looks like the producer-scrounger model described by Barnard and Sibly (1981). The scrounger individuals are usurpers of the resources found by producers. More generally, scroungers take a larger share of the food found relative to their own food-searching efforts. In our case, the high-triggering fish may play the role of the producers that feed the entire group, whereas all the others fish take advantage for food of their activity.

This study shows that the removal of the high-triggering fish is followed by a reconstruction of the group; and that the new organisation formed has the same structure and function of the initial one. The results show that this high food-demand status is important for feeding the entire group and perhaps for the group stability, but fails to explain the presence and the benefits of this function. The present study also suggests the possibility of social transmission in sea bass juveniles. Finally, the social scheme of a juvenile sea bass group in a self-feeding system looks like the producer/scrounger model, in which the scrounger individuals are usurpers of the food resources delivered by a few producers.

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Table 1. Total number of trigger actuations, average number of actuations per day and total quantity of food delivered and eaten per day by juvenile sea bass *Dicentrarchus labrax* in each control tank; and number of high-triggering (H-T) fish, low-triggering (L-T) and zero-triggering (Z-T) fish during the both period 1 and period 2.

	Tank no.	Total number of actuations	Average number of actuations/day	Quantity of food delivered (g)/day	Quantity of food eaten (g)/day	Number of H-T fish	Number of L-T fish	Number of Z-T fish
Period 1	2	1246	29.7	91.6	91.6	4 (79)	23 (19)	22 (2)
(D1 to D42)	3	1035	24.6	76.1	76.1	4 (75)	25 (23)	22 (2)
	6	854	20.3	62.8	62.8	5 (72)	25 (26)	20 (2)
Period 2	2	819	32.8	101.1	101.1	4 (81)	24 (18)	21 (1)
(D44 to D68)	3	858	34.3	106.0	106.0	4 (95)	13 (4)	34 (1)
	6	1017	40.7	125.6	125.6	5 (89)	15 (10)	30 (1)

Note: Given in parentheses in the last three columns is the relative percentage of the triggering activity (i.e. the food-demand activity).

Table 2. For each control tank, the percentage of sea bass switching between high-triggering (H-T) to low-triggering (L-T) levels; and conversely, between low- or zero-triggering (Z-T) to high-triggering levels, and the percentage of high-triggering sea bass which have a constant activity level.

Tank no.	Total number of H-T fish	Number of fish switching between H-T → L-T activity	Number of fish switching between L-T → H-T activity	Number of fish switching between Z-T → H-T activity	Number of Constant H-T fish
2	4	1	-	1	3
3	4	1	-	1	3
6	5	2	2	-	3

Table 3. Total number of trigger actuations, average number of actuations per day and total quantity of food delivered and eaten per day by juvenile sea bass in each removal tank; and number of high-triggering fish (H-T), low-triggering (L-T) and zero-triggering (Z-T) fish before (period 1) and after (period 2) the removal experiment (day 43).

	Tank no.	Total number of actuations	Average number of actuations/day	Quantity of food delivered (g)/day	Quantity of food eaten (g)/day	Number of H-T fish	Number of L-T fish	Number of Z-T fish
Period 1	1	929	22.1	68.3	68.3	3 (80)	27 (18)	20 (2)
Before removal	4	783	18.6	57.6	57.6	3 (83)	16 (29)	31 (3)
	5	829	19.7	60.9	60.9	4 (70)	22 (21)	24 (3)
Period 2	1	623	24.9	76.9	76.9	3 (87)	13 (14)	31 (2)
After removal	4	707	28.3	87.3	87.3	3 (56)	23 (25)	17 (1)
	5	823	32.9	101.6	101.6	4 (91)	16 (8)	26 (2)

Note: Given in parentheses in the last three columns is the relative percentage of the triggering activity (i.e. the food-demand activity).

Table 4. Average number of days before the first actuation of the high-triggering sea bass, before and after the removal (day 43) in the three assay tanks.

Tank no.	1	4	5	Average
Period 1	12.7 (3)	17.0 (3)	11.5 (4)	13.7
Period 2	3.7 (3)	4.3 (3)	6.3 (4)	4.8
				**

Note: Number of fish in parentheses and Student's *t*-test with the significance levels denoted by asterisks: ** $P < 0.01$.

Table 5. Initial and final average weights, and average specific growth rate (SGR) of high-triggering (H-T), low-triggering (L-T) and zero-triggering sea bass (Z-T) in all tanks monitored over 42 days for the removal tanks no. 1, 4, 5 and over 68 days for the control tanks no. 2, 3, 6.

	Initial weight (g)			Final weight (g)			
Tank no.	per tank of fish		per activity group	per tank of fish		per activity group	Average SGR (%/day)
		H-T	315 ± 55 (3)		H-T	345 ± 53 (3)	0.160 ± 0.075 (3)
1	288 ± 8 (50)	L-T	294 ± 11(27)	306 ± 8 (50)	L-T	308 ± 11 (27)	0.081 ± 0.028 (27)
		Z-T	276 ± 11 (20)		Z-T	297 ± 11 (20)	0.118 ± 0.026 (20)
			ns			ns	ns
		H-T	332 ± 30 (3)		H-T	381 ± 29 (3)	0.150 ± 0.062 (4)
4	284 ± 8 (50)	L-T	276 ± 14 (17)	306 ± 7 (50)	L-T	308 ± 11 (17)	0.231 ± 0.027 (30)
		Z-T	284 ± 11 (30)		Z-T	297 ± 9 (30)	0.247 ± 0.056 (14)
			ns			*	ns
		H-T	310 ± 15 (5)		H-T	330 ± 16 (5)	0.154 ± 0.021 (4)
5	295 ± 7 (50)	L-T	307 ± 10 (22)	296 ± 8 (50)	L-T	307 ± 12 (22)	0.187 ± 0.033 (24)
		Z-T	279 ± 10 (23)		Z-T	279 ± 11 (23)	0.134 ± 0.030 (23)
			ns	ns		ns	ns
		H-T	304 ± 23 (4)		H-T	370 ± 39 (4)	0.222 ± 0.084 (3)
2	279 ± 7 (49)	L-T	282 ± 9 (30)	343 ± 9 (49)	L-T	344 ± 10 (30)	0.192 ± 0.035 (17)
		Z-T	263 ± 13 (14)		Z-T	335 ± 19 (14)	0.083 ± 0.029 (30)
			ns			ns	*
		H-T	315 ± 34 (4)		H-T	362 ± 40 (4)	0.098 ± 0.023 (5)
3	287 ± 9 (51)	L-T	278 ± 12 (24)	332 ± 10 (51)	L-T	328 ± 12 (24)	-0.012 ± 0.025 (22)
		Z-T	291 ± 13 (23)		Z-T	331 ± 17 (23)	-0.003 ± 0.033 (23)
			ns			ns	ns
		H-T	296 ± 28 (5)		H-T	359 ± 27 (5)	0.224 ± 0.072 (5)
6	282 ± 7 (50)	L-T	278 ± 10 (25)	333 ± 8 (49)	L-T	329 ± 11 (24)	0.193 ± 0.027 (25)
		Z-T	284 ± 12 (20)		Z-T	331 ± 13 (20)	0.177 ± 0.022 (20)
	ns		ns	ns		ns	ns

Note: *n*, number of fish in parentheses. Analysis of variance (ANOVA) with the significance levels denoted by asterisks: * $P < 0.05$, ns = no significance.

Figure legends

Figure 1. Di-Poi et al. Diagram of the self-feeding system; sea bass *Dicentrarchus labrax* actuated the food dispenser and PIT registration unit while data were collected on a computer.

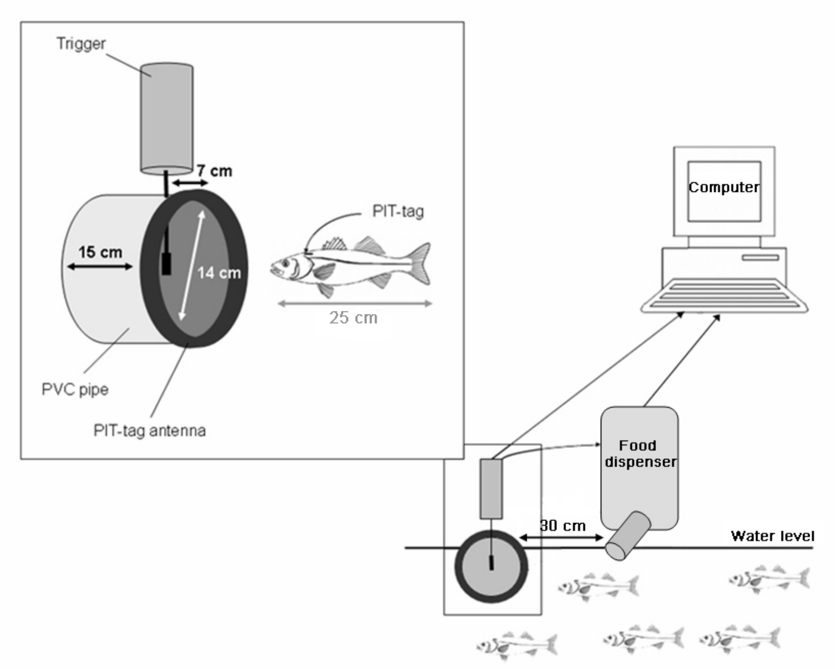

Figure 2. Di-Poi et al. 3-D plot of the daily triggering activity (i.e. food-demand activity) of each sea bass *Dicentrarchus labrax* in the three control tanks no.2 (a), no.3 (b) and no.6 (c) during the 68-day experiment. Fish displaying a constant high-triggering activity are represented in dark grey. Fish displaying a transitional high-triggering activity are in light grey. The low-triggering fish are indicated in white and the remaining fish are the zero-triggering individuals.

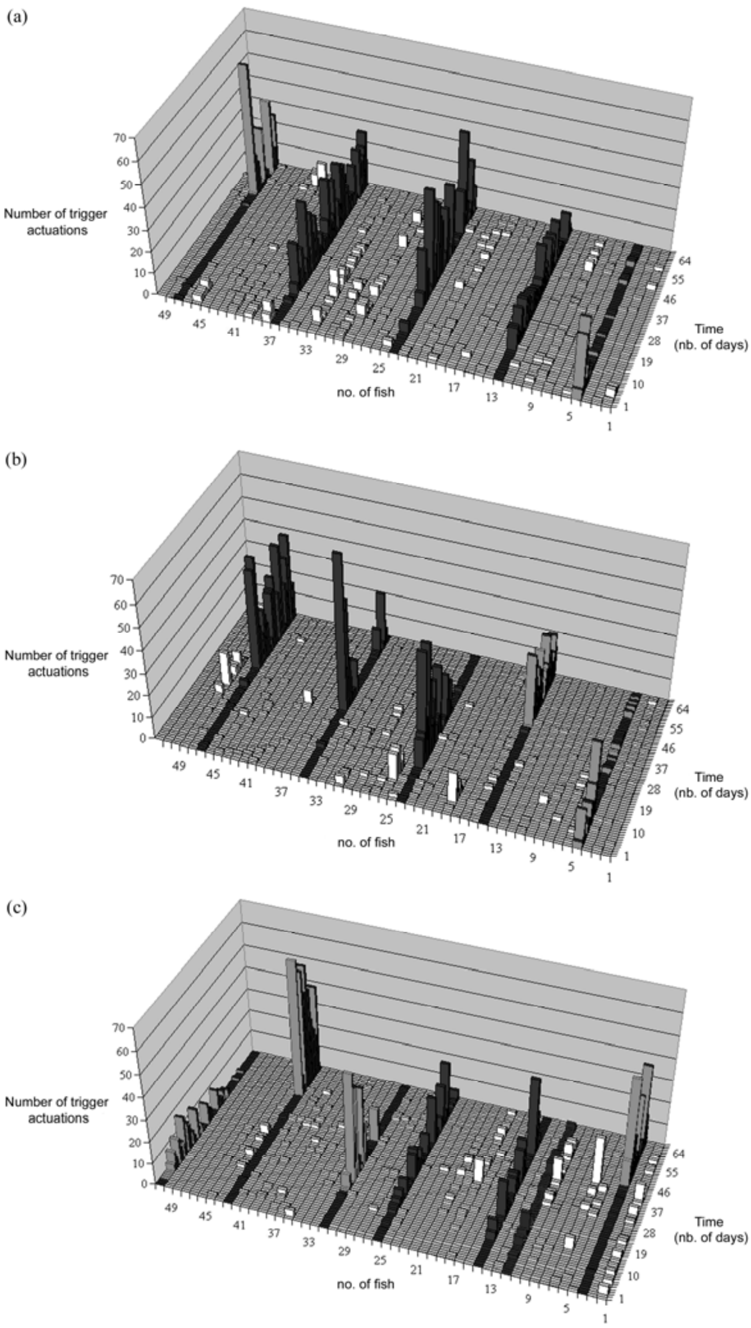

Figure 3. Di-Poi et al. 3-D plot of the daily triggering activity (i.e. food-demand activity) of each sea bass in the three removal tanks no.1 (a), no.4 (b) and no.5 (c) in which a removal experiment was performed at day 43. Fish displaying a high-triggering activity are represented in dark grey. Their removal is indicated at day 43 and represented by the white bands. The new high-triggering fish are represented in light grey. The low-triggering fish are indicated in white plots and the remaining fish are the zero-triggering individuals.