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Changes in behavioural response of Mediterranean seabass (*Dicentrarchus labrax* L.) under different feeding distributions

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Abstract

Captive-induced behavioural deviations may involve many aspects of fish behaviour such as swimming activity and enhancement of individual aggressiveness. We studied seabass (*Dicentrarchus labrax*) behaviour as a function of manual and automatic feeding distribution modes. Under manual mode, the food is distributed over an extended area for a longer period, and its precise location is not always predictable, while with pneumatic automatic feeders, fish receive the same amount of resource, which is concentrated in the same surface area over a shorter period. We compared seabass behaviour under automatic and manual conditions collecting video image recordings before, during, and after feeding distribution, in the morning and in afternoon, on two different days, and analysing data within independent sessions of measurements. Feeding modes significantly affected swimming behaviour: automatically-fed fish were characterised by vertical movements through the water column (towards the surface and bottom) and by horizontal swimming. Manually-fed fish were instead characterised by sharp direction changes during their swimming, mostly towards the surface. Feeding distribution induced changes in collision frequency and elicited aggressive behaviour. In particular, agonistic behaviour (i.e. a fish attacks another fish) was almost exclusively recorded during the feeding under automatic distribution, whereas it was constantly expressed during all the distribution phases under manual mode.

Introduction

Captivity in cultivated fish might involve sim-

ple alterations of swimming activities (Hammer, 1997; Bégout Anras *et al.*, 2004), feeding capacities (Andrew *et al.*, 2004a), or enhancement of individual aggressiveness as evidenced in rainbow trout, in salmon and in both European seabass (*Dicentrarchus labrax*) and seabream (Magnuson, 1962; Ruzzante, 1994; Adams and Huntingford, 1996; Kadri *et al.*, 1997; Adams *et al.*, 1998; Andrew *et al.*, 2002; Ellis *et al.*, 2002; Andrew *et al.*, 2004b; Kristiansen and Ferno, 2006; Noble *et al.*, 2007a, 2007b). Some studies on captive fish have tested that foraging activities can be influenced by the food distribution mode used. For example, a large study carried out in Greece and Spain with seabream and seabass showed that on-demand feeding regime, compared with the pneumatic feeding, was particularly efficient in reducing competition (Andrew *et al.*, 2002), aggression (Noble *et al.*, 2007b) and improving, in turn, the growth (Azzaydi *et al.*, 1999).

However, although the major efficiency of on-demand feeding regime has been largely demonstrated also in Atlantic species (e.g. salmon; Noble *et al.*, 2007a, 2007b and many references therein), most Mediterranean fish farmers still use mainly two different feeding modes, the manual one in smaller circular open and the centralised automatic mode in larger cages (e.g. Farm-Ocean Inc., Bergen, Norway). Under manual feeding regime, food is distributed by hand over an extended area (over 50% of the whole available surface of the cage) for a longer period (20-30 minutes) until satiation (i.e. until no fish feeding was observed at surface), and its precise location is not always predictable. In contrast, with pneumatic automatic feeding systems, fish always receive the same amount of food concentrated in the same surface area (not larger than 2-6 m of diameter) for shorter periods (about 45 times of 2 minutes each), both in early morning and late evening. Satiation of fish, in this case, is assumed on the basis of studies that provide results on the food to be delivered allowing the most efficient fish growth to the market size (Paspatis *et al.*, 1999). Although altered behaviour in response to automatic feeding has been already demonstrated (Andrew *et al.*, 2002), behaviour under manual feeding regime has never been studied in Mediterranean species like seabass.

This investigation would be of particular importance when assessing the choice of distribution mode to be adopted by fish farmers to optimize their activities efficiency. Accordingly, the main aim of this study was to test whether two different modes of food distribution had a differential effect on its behavioural responses in the form of i) water column position and swimming, ii) the number of casual collisions,

and lastly iii) the number of attacks as an expression of aggressiveness.

Materials and methods

Study area, rationale and sample collection

The study was carried out in October-November 2004 in the Gulf of Castellammare, at the northern coast of Sicily (latitude 38° 02' 31" N; longitude 12° 55' 28" E) when the temperature of seawater was about 21°C. Gulf waters are known as highly oligotrophic (CHL-a concentrations lower than $1.0~\mu g~L^{-1}$), with a low degree of turbidity (nephelometric standard unit <5 and Secchi disk depth up to 25 m throughout the year) and low current velocity ($\sim 12~cm~s^{-1}$; Sarà *et al.*, 2006). Experiments were carried out in large cages (Farmocean, Norway; volume=4,500 m³) and in circular cages (volume=1,000 m³), which were positioned in the Eastern part of the Gulf (latitude 38° 04' 53" N; longitude 13° 02' 04" E) and moored to the bottom at a depth of about 32 m, about 0.7 nm off the coastline. The cages were filled with seabass (*Dicentrarchus labrax*) of the same size (~280-300 g) and at the same density (~20 kg m³; about 66 fishes per m³). In both cage types, the supplied food was produced by BioMar (France)

Table 1. Description of swimming behaviours of seabass.

Behavioural categories	Behaviour description
Surface position	Fish at <3 m from surface
Middle column position	Fish at 3-5 m from surface
Horizontal swimming	Fish move parallel to surface
Swimming vs. surface	Fish move vertically toward surface
Swimming vs. bottom	Fish move vertically toward bottom
Direction change	Fish modify their swimming pathway
Collision	Physical contact between two fishes, which swimming direction was not pointed toward the other
Agonistic	Physical contact between two fishes after, at least, one of them moved with its head pointed toward the other

Table 2. Behavioural frequencies (mean ±SE) during food distribution.

	Feeding distribution	
	Automatic	Manual
Behavioural events	Mean±SE	Mean±SE
Surface position	2.2±0.4	2.2±0.4
Middle column position	3.1±0.3	2.1±0.3
Horizontal swimming	35.1±0.9	26.5±1.1
Swimming vs surface	10.4±0.6	8.1±0.5
Swimming vs bottom	22.1±0.7	20.3±0.4
Direction change	16.2±0.9	30.1±0.6
Collision	8.2±0.6	9.6±0.8
Agonistic	2.7±3.1	1.1±3.4

and Hendrix (Italy).

The food was supplied automatically in the large cages and by hand in the circular cages. In both cases, the total daily amount of food was divided in two meals. The first meal was early in the morning (8:00 a. m.; hereafter the a.m. period), while the second one was provided in the afternoon (3:00 p.m.; hereafter the p.m. period). In the case of submersible cages, about 400-500 kg of food per meal was supplied through an automatic pneumatic feeding system (hereafter automatic mode, 800-1000 kg per day). The time length of each meal distribution was about 2 hours both in the a.m. and p.m. periods. During each meal, the food was supplied in 3 kg bouts every 2-3 minutes until the end of the programmed food amount. In manual distribution (hereafter manual mode), the total amount of food (about 200 kg per day) was provided by hand by an operator in about 30 minutes for each meal. The food available to each fish per delivery was on average 4-6% of wet weight (Mazzola and Rallo, 1981), which is the amount considered to satiate Mediter-ranean cultivated fish and to allow their fastest growth in the shortest period of time.

The experiments consisted in the collection of video images by SONY Hi-8 video cameras encased in waterproof boxes (NIMAR Inc., Italy) fixed inside the submersible and circular cages at a depth of about 1.5 m beneath the surface.

Collection of video images lasted 30 minutes before the meal (hereafter the before phase), 30 minutes during the meal (hereafter the during phase), and 30 minutes after the meal (here-after the after phase). The experiment started one hour after the placement of cameras inside the cages to allow the fish to acclimate to the presence of the cameras and to avoid any inter-ference due to the human presence. In automat-ic mode, once recording of the before phase was carried out, the meal started to be provided for at least 3 hours. In this phase (during the meal), video images were recorded for a period of 30 minutes chosen in the middle of the meal. The after phase started once the meal finished, and lasted for another 30 minutes. In the case of manual mode, operators reached the cages, positioned cameras, then moved out of sight in a boat anchored upstream at about 30 meters from the cage, waited for 1 h to allow the fish to acclimate to the presence of the cameras and to avoid any interference due to the human pres-ence, and then the session started (before phase). At the end of the before phase, operators moved close to the cages by pulling a rope, and then they started supplying food for about 30-40 minutes; once finished with the meal, the oper-ators moved away from the cages. The experi-ments were repeated on two different days, with an interval of at least 7 days. Video images were analysed in the lab and each 30 minutes of video

recording was divided into two sessions of 15 minutes each. Within each session, we choose 75 two-second frames randomly extracted by using the digit tables (Zar, 1999). The two-sec-ond frames represented the best compromise to observe a fish moving throughout the image field on the TV screen. During each frame, we followed the behaviour of at least 60 fishes (i.e. repeating the vision of frame 60 times), and the occurrence of each category was counted in all 60 fish and then transformed into a frequency. Table 1 shows the list of behavioural categories recorded as single events. Positioning at the surface or in the middle of the water column were considered as the expression of general position in the cage, whereas swimming behav-iour was composed by horizontal swimming, swimming towards the surface, swimming towards the bottom, and direction changing.

Statistical analyses and elaborations

Behavioural data were analysed in order to test the null hypothesis, i.e. that there was no difference in fish position in the water column, or swimming behaviours under different feed-ing modes (automatic *vs* manual distribution) using a three-way PERMANOVA (Permutational Multivariate Analysis of Variance) design (Anderson, 2001) on square root-transformed percent matrixes, using the Euclidean distance and 9999 permutations. Thus, FEEDING (FEED: automatic *vs* manual distribution, 2 levels), PERIOD (PER: feeding in the morning [a.m.] *vs* feeding in the afternoon [p.m.], 2 levels), and PHASE (PH: before, during, and after distribu-tion of feed, 3 levels) were treated as fixed fac-tors in the experimental design. Two different and independent days of measurement (Day, 2 levels) were treated as random factors and nest-ed in the interaction FEED x PER x PH, while four different sessions of measurement were treated as random and orthogonal factors (Session, 4 levels). The homogeneity of multi-variate dispersions was tested by the PERMDISP test (Anderson, 2006). A similar experimental design was used to test the same hypothesis of two other variables (collisions and agonistic behaviours). In this case, the homogeneity of variance was tested with the Cochran's C test and Student-Newman-Keuls was used as a post-hoc-comparison test (Underwood, 1997). Statistical analyses were performed by means of the software PRIMER 6 plus PERMANOVA (Clarke and Warwick, 1994; Anderson, 2006; personally licensed to Chiara Romano; National Research Council, Italy) and GMAV 5.0 (University of Sidney, AU; personally licensed to Gianluca Sarà).

Table 3. PERMANOVA carried out on water column position and swimming variables to test the null hypothesis of no difference between automatic and manual modes throughout different phases of the study (BEFORE, DURING, and AFTER).

		Water column position			Swimming		
Source of variation	df	MS	Pseudo-F	$P_{(perm)}$	MS	Pseudo-F	$P_{(perm)}$
Feeding (FEED)	1	4.11	0.71	ns	609.28	13.76	**
Period (PER)	1	30.44	3.55	*	131.39	3.03	**
Phase (PH)	2	42.65	4.88	**	400.75	8.72	**
Session	3	2.78	1.07	ns	12.04	1.17	ns
FEED x PER	1	5.55	0.69	ns	128.64	3.16	**
FEED x PH	2	3.74	0.74	ns	38.72	0.99	ns
FEED x Session	3	1.86	0.72	ns	14.94	1.46	ns
PER x PH	2	6.70	0.97	ns	16.29	0.61	ns
PER x Session	3	1.71	0.66	ns	16.60	1.62	ns
PH x Session	6	1.67	0.65	ns	17.03	1.66	*
FEED x PER x PH	2	0.93	0.39	ns	43.53	1.27	ns
FEED x PER x Session	3	4.18	1.61	ns	13.80	1.34	ns
FEED x PH x Session	6	0.92	0.36	ns	19.30	1.88	*
PER x PH x Session	6	1.99	0.77	ns	13.39	1.30	ns
Day (FEED x PER x PH)	12	7.61	2.94	**	30.10	2.93	**
FEED x PER x PH x Session	6	1.51	0.58	ns	12.20	1.19	ns
Day (FEED x PER x PH) x Session	36	2.59	1.59	**	10.27	1.31	**
Residuals	288						

ns = no significant difference; *= difference at P<0.05; **= difference at P<0.001.
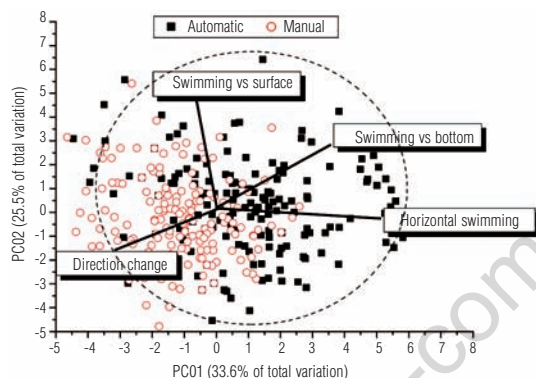
Figure 1. Principal coordinate analysis (PCO) of swimming behaviour comparing automatic vs manual distribution modes.

Results

Measures of behavioural variables recorded under different treatments are reported in Table 2. The feeding regime did not affect the position of the fish in the water column (Table 3). Instead, the position of fish groups changed significantly between periods of the day (a.m.>p.m.; P<0.05): fish mostly stayed in the middle of the water column in the morning, whereas they typically stayed close to surface in the afternoon. Further, they moved from the middle column during the food distribution phase (P<0.05) and returned to this position in the before and after phases. As a general picture, swimming behaviour was significantly affected by feeding distribution modes (Table 3; Figure 1) as automatically-fed fish were significantly characterised by vertical movements through the water column (towards the surface and bottom) and by horizontal swimming. Manually-fed fish were instead significantly characterised by sharp direction changes during their swimming, mostly towards the surface (P<0.05). These differences among groups were maintained both in the a.m. and p.m. phases of the day (PERMANOVA pairwise test P<0.05) and throughout both the before and after phases (Figures 2a and 2b; PERMANOVA pairwise test P<0.05). Under automatic distribution, the overall behavioural responses during each feeding phase were different, as before the food arrived, fish were mostly swimming at the surface horizontally, during food distribution they showed quick vertical swimming, and finally, in the period after they swam horizontally some meters beneath the surface (P<0.05). Under manual distribution, the overall response during the food distribution was characterized by constant direction changes that resulted in a significant difference (P<0.05) compared with the overall response expressed before and after

feeding, which was characterized by both swimming beneath the surface and minor direction changes (P>0.05).

The feeding distribution elicited aggressive behaviours and induced changes in collision frequency among fish (Table 2). Under automatic distribution, collisions were significantly higher during feeding than before and after phases (Figure 3a). Under manual distribution, collisions were less frequent during the before phase, whereas they were elicited throughout the during phase, and still maintained higher during the after phase (see SNK test inside Figure 3a). Agonistic behaviour (i.e. a fish attacks another fish) was basically elicited in the during phase under automatic distribution, and almost absent in the before and after phases (ANOVA, P<0.05; Figure 3b). Under manual distribution, no difference in agonistic behaviour was observed (Figure 3b) among feeding phases.

Discussion

In the investigated Sicilian farm, seabass showed significant changes of behaviour under two different investigated feeding distribution modes. Specifically, from the analysis of the behavioural responses, it was evident that fish responded differently to manual and automatic feeding modes during periods of food distribution and the periods just preceding and/or following it. Further differences were also recorded between the responses occurring with daylight (a.m.) and the ones occurred in conditions of subdued light (p.m.) (Blyth *et al.*, 1999). The position in the water column was not affected by feeding distribution as fish occupied the layers in the cages in the same way under automatic and manual distribution. However, they responded to different day phases, as they occupied deeper layers in the morning, then moved towards superficial layers in the evening. This observation is in accordance with evidence in the literature indicating that seabass prefer to occupy surface layers in experimental conditions (Schurmann *et al.*, 1998). Since most fish farmer activities occur in the morning, the preference for deeper water column layers might be simply explained as an avoidance response to noisy manoeuvres (i.e. boat engines approaching cages, farmers walking and shouting on gangways around cages; Richardson *et al.* 1995; Sarà *et al.* 2007).

Swimming behaviour was basically affected by different food distribution modes. Automatically fed fish were mainly characterised by circular horizontal swimming around a restricted central area of the cages (i.e. exact-
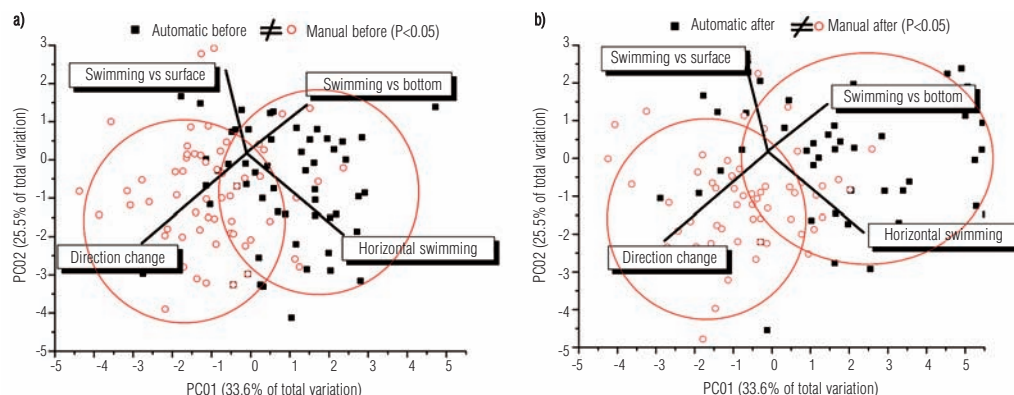
Figure 2. Principal coordinate analysis (PCO) analysis of swimming behaviour comparing automatic *vs* manual distribution modes in a) a.m. periods and b) p.m. periods.
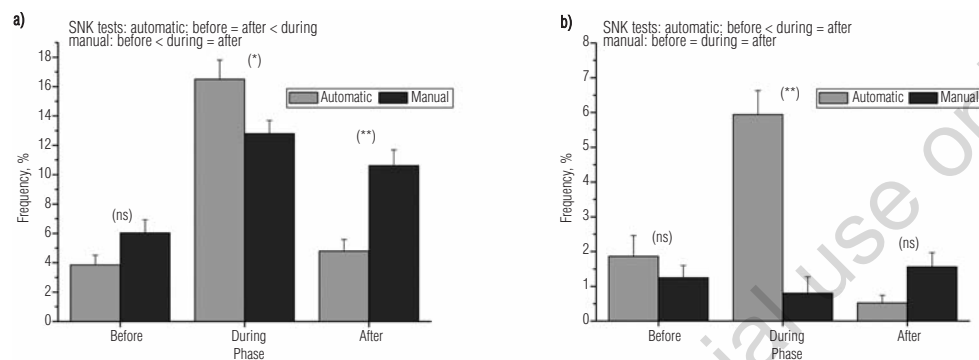
Figure 3. Frequency of a) collisions and b) agonistic behaviours comparing automatic vs manual distribution modes throughout before, during and after phases (Student-Newman-Keuls [SNK] post-hoc-comparison tests are reported inside graphs.

ns= no significant difference; *= difference at P< 0.05; **= difference at P< 0.01).

ly where the food usually fell from the pneumatic feeders) and by sudden and continuous vertical micromovements (of tens of centimetres), from the surface to deeper layers and vice-versa (Hammer, 1997). These movements strictly occurred below the surface where the sinking pellets fell. Conversely, manually-fed fish were characterised by continuous direction changes (i.e. turning behaviour; Noble *et al*. 2007a, 2007b; Sarà *et al*., 2007) across the larger area of feed supply in the cage, indicating a response to the spreading of food by farmers. This type of behaviour was maintained over time in both the before and after phases, in the a.m. and p.m. periods. Behaviour of manually-fed fish appeared to be responsive not to limited resource availability (i.e. the proviso in production farms is that food should be provided until satiation of each fish), but to the high unpredictability of the whereabouts of the food supplied. Random searching of food which position is not predictable would, in fact, induce fish to remain close to the surface, continuously swimming with significant levels of turning behaviour. This would cause an increasing of energy expenditure which, *in ultimis*, may have effects on growth performances reducing economic incoming for farmers (Andrew *et al.*, 2002; Noble *et al*., 2007a, 2007b). Automatic mode behaviour could have induced a foraging strategy which characteristics were imposed by an extreme competition triggered by high density of individ-

uals restricted within a small, as predictable, food patch (Paspatis *et al*., 1999; Andrew *et al*., 2002). The food amount delivered in automatic mode is chosen to assure fish satiation (Paspatis *et al*., 1999) and, therefore, to allow fish farmers to benefit of a profitable aquaculture activity. The same amount delivered over and over, however, did not reduce agonistic behaviours, which function has been explained to be a hard-wire response to cope, in constrained conditions, with despotic individuals with better competitive abilities (Messier *et al*., 1990; Hawkins *et al*., 2005; Purchase and Hutchings, 2008). An automatic schedule would elicit the conditioned behaviour that rewards fish remaining in the feeder supply area and moving continuously around it (Andrew *et al*., 2002; Huntingford and Adams 2005). This result, along with the differences recorded in the automatically-fed fish, substantiates that rearing conditions may induce aberrant behaviours particularly when captivity regimes provide settings disrupting natural biological rhythms (Bégout Anras and Lagardere, 2004). The automatic food distribution mode also enhanced collisions and aggressive behaviour. Automatically-fed fish significantly reduced their inter-individual distances during food distribution, but they recovered their usual behaviour (i.e. a lower number of collisions similar to the before phase) within a few minutes after the end of feeding. In contrast, the frequency of collisions under manual

mode was lower than automatically-fed fish, but these fish maintained a higher frequency of collisions for a longer time after the end of feed distribution, recovering the former behaviours slower than fish fed in automatic mode. The increase in collisions under rearing conditions has been documented in many farmed species (e.g. rainbow trout; see Ellis *et al*., 2002) as it seems a regular effect of over-crowding and is favoured by the limited availability of space when the feed source is pulsing (i.e. automatic distribution). In contrast, when the food is spread over a larger area (i.e. manual distribution), collisions were reduced. However, it is not clear why the recovery time was slower under manual than automatic distribution and this deserves further research.

The condition of differential access to food implicitly involved a higher level of aggressiveness under automatic distribution. Thus, while agonistic responses were higher in automatic than manual mode, they were restricted to the during phase only. In the after phase, fish attacks waned within a few minutes, suggesting that aggressiveness was related only to the access to food. Thus, if other behavioural traits like continuous circular swimming in automatically-fed fish and direction change in manually-fed fish appeared to be maintained over time throughout all phases of this study, agonistic traits were limited to situations when fish competed for resources under automatic feed mode.

Conclusions

In conclusion, present results suggest that captive seabass responded i) differently to manual and automatic feeding modes during periods of food distribution and the periods just preceding and/or following it and ii) the response was different between day phases (a.m. vs p.m.). Also, the aggressiveness seems to be limited only when it results in an increased chance to access the resource which is consistent with the literature suggesting that domestication can sometimes influence aggressiveness (Huntingford and Adams, 2005), and that the direction of its effect depends on feeding regimes (Ruzzante, 1994). Different conditional processes modes used to feed our seabass induced different behavioural changes (e.g. increased aggression and conditioned swimming activity), which were maintained over time potentially impairing the welfare of cultivated fish.

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