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Exploration behaviour and flight response toward a stimulus in three sea bass strains (*Dicentrarchus labrax* L.)

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Abstract:

Domestication and selection may affect fish behaviour, sometime as soon as at the first generation of domestication. However, knowledge about how both processes impact on fish spatial exploration and swimming activity still is to be improved. The objective of this experiment was (i) to evaluate spatial exploration behaviour and swimming activities of three sea bass strains having different domestication and selection levels and (ii) to analyse their responses to an acute stress. Sea bass exploration and swimming activities were studied before, during and 40 min after a stimulation (standardized fall of an object). The experimental tank was divided in to four zones, and the time spent, the distance travelled in each zone and the swimming complexity were quantified for each period from video recording. Results showed that fish from all strains presented the same flight response and that stimulus exposure induced a significant decrease in exploratory behaviour and swimming activity. The present study has also demonstrated that only one generation of captivity could be sufficient to obtain fish presenting the same behavioural characteristics than fish reared since at least two generations. Moreover, this study has highlighted that selection for growth seemed to select fish characterized by a bolder personality and potentially better adapted to rearing environment. It allowed us to suggest that selection for growth may have a higher effect on fish personality than domestication only.

Keywords: Domestication; Selection; Personality; Swimming activity; Danger avoidance; Risk assessment; Thigmotaxis

1. Introduction

In wild ecosystems, swimming behaviour of fish is very important for feeding, migrating or for escaping a predator (Wardle, 1993). That is also important in a captive environment where it influences access to food, adaptation to water flow rate and good positioning in the group. It is already established that chronic stress (*e.g.* change of water temperature, hypoxic conditions, photoperiod), or repeated acute stress (*e.g.* handling), modifies swimming velocity (Kristiansen et al., 2004; Olla and Studholme, 1971). Moreover, domestication and selection could have a rapid impact on fish behaviour, some time as soon as at the first generation of domestication (Bégout Anras and Lagardère, 2004; Huntingford, 2004; Vandeputte and Prunet, 2002). However, knowledge about how both processes impact on fish spatial exploration and swimming activity still is to be improved. Although, standardized stimulation has been mostly used to study the flight response in fish and particularly the "C-start" response in relation to different environmental constraints (group *versus* solitary response, Domenici and Batty, 1997; pollution, Faucher et al., 2006; water temperature, Johnson et al., 1996; hypoxia, Lefrançois and Domenici, 2006), few studies were focussed on the impact of domestication (Fernö and Järvi, 1998; Malavasi et al., 2004, 2008; Petersson and Järvi, 2006) and, to our knowledge, none targeted the impact of selection for growth on exploration behaviour. Main goal of the previous studies was to evaluate the domestication effect on juvenile fish survival and consequently their relevance for the enhancement of restocking programmes.

The present study had a different goal. It used the analysis of sea bass spatial exploration behaviour and swimming activity level to determine whether three strains of sea bass (issued from wild, domesticated and selected for growth parents) differed in their response to an acute stressor. Hereafter, we have evaluated the influence of domestication and selection process on risk taking behaviour and thus on fish personality (bold or shy; Fraser et al., 2001; Wilson et al., 1993, 1994). Accordingly, the purpose of this work was to measure the basic locomotory activity and the disorders induced by a standardized stressor. Sea bass spatial exploration behaviour and swimming activity level were thus monitored before, during and 40 min after a standardized stimulation. Fish were video-recorded and their spatial exploration behaviour (spatial distribution and time spent), their swimming activity level

(distance travelled) and their swimming path complexity (angular velocity) were analyzed in each tank zone and during the three periods.

2. Material and methods

2.1. Animals

The experiment was conducted on 84 fish from three strains (28 fish per strain). The three tested strains have been hatched and reared at the experimental research station of Ifremer in Palavas-les-Flots (France). They are issued from a full factorial crossing (each dam is crossed with each sire) of 13 wild Mediterranean dams with 20 Atlantic wild sires (*Wild* strain), 20 Atlantic domesticated sires (*Domesticated* strain) and 19 Atlantic selected sires (*Selected* strain) respectively. The *Wild* sires were chosen among an Atlantic wild population kept in captivity for a least one year. The domesticated sires have been obtained by choosing fish at random in a population reared for two years according to sea bass rearing standards (Chatain, 1994) while the selected sires were the 5% longest fish at the same age (20 months, 400 g) in this same population. Thus all fish tested in this experiment never experienced the natural environment, had the same life history except that their parents presented different levels of domestication and selection. To summarize, *Wild* strain was characterized by fish issued from wild parents with at least on year in captivity, *Domesticated* strain by parents with one generation of captivity (*i.e.* domestication) and *Selected* strain by parents with one generation of domestication and one generation of selection for growth.

At the beginning of the study, fish were around 20 month-old with an average initial body weight of 234.8 ± 9.5 g for *Wild* (coefficient of variation (CV) = 21%, n = 28 fish), of 267.2 ± 9.1 g for *Domesticated* (CV = 17%, n = 28 fish) and of 235.7 ± 9.5 g for *Selected* (CV = 21%, n = 28 fish). The fish weight were not statistically different ($F_{2,80}$=1.46, p>0.05).

2.2. Experimental set up

The experiment was carried out in a 400 l tank similar to the ones used to maintain the experimental fish. Water temperature was maintained at 20.2 ± 1.5°C, oxygenation above 90 % saturation in the

outlet and salinity 21.2 ± 1. Tank was sheltered by black curtains and highlighted by three spotlights located to minimise shadow. The stimulus was a tube full of sand of 67 g, 96 mm length and 25 mm diameter, which fall was driven by an electromagnet (Fig.1A). An opaque pipe (1.6 m length, 35 mm diameter) was fixed 2 cm above the water surface to hide the stimulus during its fall and to allow the recording of the fish reaction at the moment of impact (Fig. 1A). A Mini color CMOS camera (Velleman) was located at 1.6 m of the water surface and video were recorded on a hard disk recorder (Fig.1A).

2.3. Behavioural test

A single fish was quickly moved from its maintenance tank to the experimental tank two hours before the experiment started. According to Marino et al. (2001) a capture and handling procedure of short duration in two year old hatchery sea bass did not induce any significant variation in blood parameters, such as serum glucose or cortisol. Even if the procedure to place fish in the experimental tank involved stress, the procedure was standardized for each fish and thus allowed to evaluate the swimming responses for each individual in the same way.

Video recording begun 30 min before starting the test and fish homogeneous swimming in the entire tank was required before stimulation. The stimulus was dropped by releasing the electromagnet when the fish reached the stimulation zone (Fig.1B). Fish behaviour was recorded during one hour after the stimulation (Fig.2). Fish which never swam in the tank and which thus could not be stimulated were characterised as “shy” fish. Fish which presented a homogeneous swimming in the tank and which could be stimulated were characterised as more “bold” and their exploration behaviour was further analysed.

After the test, fish were removed from the experimental tank and placed in a separate tank to avoid alarm pheromone release within the fish group which remained to be tested.

2.4. Video analyses

The video recordings were analysed using the software EthoVision Color Pro version 3.1.16 (Noldus, The Netherland), which allowed to separate the tank in 4 virtual zones of the same surface (Z1, Z2, Z3 and Z4; Fig.1B) and to track the fish swimming behaviour (Fig.2).

Each video recording were analysed in 3 sequences of 20 min:

- sequence 1 (S1): before the stimulation
- sequence 2 (S2): just after the stimulation
- sequence 3 (S3): 40 min after the stimulation

2.5. Statistics

Different variables of interest were chosen to analyze the fish behaviour:

- The time taken from the start of recordings to the moment of the stimulation. This variable allowed to measure individual latency before stimulation.
- The proportion of time spent by a fish in each zone (residence; in %). This variable allowed to identify the fish spatial distribution for each sequence.
- The distance travelled by each fish in the tank (in cm). This variable quantified the fish swimming activity level in the tank for each sequence.
- The fish angular velocity weighted by the time spent by the fish in each zone (in degrees.s^{-1}). This variable was calculated for each fish as followed: $[(T_{Z1}xAV_{Z1})+(T_{Z2}xAV_{Z2})+(T_{Z3}xAV_{Z3})+(T_{Z4}xAV_{Z4})]/(T_{Z1}+T_{Z2}+T_{Z3}+T_{Z4})$ where T_{Z1}, T_{Z2}, T_{Z3} and T_{Z4} were the time spent by the fish in each zone (s) and AV_{Z1}, AV_{Z2}, AV_{Z3} and AV_{Z4} were the individual angular velocity in each zone (degrees.s^{-1}). This variable was an indicator of the speed of changing direction and quantified the swimming path complexity in relation to time spent by fish in each zone.

All data were analyzed for normality with a Shapiro-Wilk test and for homoscedacity of variance with a Bartlett's test; they all complied the rules for parametric statistics. Then, for the individual latency before stimulation a one way ANOVA was used to compare the difference between strains. For the fish spatial distribution, since tank zones were not independent a 2 fixed factors ANOVA was used to

compare the differences between strains and sequences for zones 1 and 4. A null model of space use was tested: the fish spatial distribution was compared to a theoretical homogeneous distribution in Z1 and Z4 (25% in each zone) by a Kolmogorov-Smirnov test. Similarly, the fish swimming activity was compared to a theoretical homogeneous activity in Z1 and Z4 (25% in each zone) by a Kolmogorov-Smirnov test. For the fish swimming activity level and swimming path complexity a 2 fixed factors ANOVA was used to compare the differences between strains and sequences. Homogeneous groups were determined with the *a posteriori* Newman and Keuls test (Dagnélie, 1975). For all tests, significant threshold was $p< 0.05$ and analyses were performed using Statistica software.

3. Results

3.1. Proportion of stimulated fish

The experiment was carried out on 28 fish of each strain. For the *Wild* strain, 16 fish (57%) placed in the experimental tank could be stimulated, for the *Domesticated* strain 14 fish (50%) and for the *Selected* strain 18 fish (64%). The remaining fish could not be stimulated because either they were motionless near a tank wall or they swam close to the walls opposite to and never reached the stimulation zone. These fish were thereafter characterized as “shy” fish and excluded from the statistical analysis.

3.2. Individual latency before stimulation

After the acclimatization time (2 hours), the latency before fish stimulation was 13.3 ± 2.7 min (± SE) for *Wild* strain, 9.9 ± 2.8 min for *Domesticated* strain and 8.7 ± 2.7 min for *Selected* strain. The three strains responses were not different ($F_{2,44}=0.82$, $p>0.05$).

3.3. Spatial distribution

On all video recorded, 16 on *Wild* fish, 11 on *Domesticated* fish and 16 on *Selected* fish could be analysed (N= 43).

There were no spatial distribution difference between strains for Z 1 ($F_{2,120}$=0.59, p>0.05) and for Z4 ($F_{2,120}$=0.99, p>0.05). However, the time spent by fish changed over time in Z1 ($F_{4,120}$=12.96, p<0.001) in for Z4 ($F_{2,120}$=16.98, p<0.001; Fig.3). Indeed, in Z1, fish spent more time during S1 (30 ± 2%) than during S2 and S3 (14 ± 3% for both) and in Z4, fish spent more time during S2 (62 ± 4%) and S3 (53 ± 5%) than S1 (29 ± 3%). During S1 the fish spatial distribution corresponded to theoretical homogeneous spatial distribution (25% per zone) for Z1 (D = 0.500, p>0.05) and for Z4 (D = 0.500, p>0.05). During S2 and S3 the observed fish spatial distribution were different than the theoretical homogeneous spatial distribution (D = 0.600, p<0.05 for Z1 and D = 0.900, p<0.001 for Z4).

3.4. Swimming activity

For all strains, fish travelled more distance during S1 (9480±1090, 9554±1522 and 11761±914 cm for *Wild*, *Domesticated* and *Selected* fish respectively) than during S2 (2798±538, 2665±1267 and 7190±1413 cm for *Wild*, *Domesticated* and *Selected* fish respectively). During S3, the distance travelled increased (4892±1302, 4741±2415 and 7503±1041 cm for *Wild*, *Domesticated* and *Selected* fish respectively) but stayed at a lower level than during S1 ($F_{2,120}$=19.32, p<0.0001; Fig.4). For each sequence, *Selected* fish travelled more distance than *Wild* and *Domesticated* fish, which were not different ($F_{2,120}$=6.87, p<0.001; Fig.4). There was no significant interaction between sequence and strain factors ($F_{4,120}$=0.32, p>0.05) which underlined an homogeneity in strains responses to the standardized stressor. During S1, fish swimming activity was not different from the theoretical homogeneous swimming activity in Z1 and Z4 (D= 0.500, p=0.112). During S2 and S3, fish swimming activity in Z1 were not different from the theoretical homogeneous swimming activity, however they differed in Z4 (D= 0.800, p<0.01 for S2 and D= 0.900, p<0.001 for S3).

3.5. Swimming path complexity

For all strains, fish changed direction slower during S1 (24±6, 34±17 and 11±3 degrees.s^{-1} for *Wild*, *Domesticated* and *Selected* fish respectively) than during S2 (145±16, 137±31 and 70±21 degrees.s^{-1} for *Wild*, *Domesticated* and *Selected* fish respectively).

During S3, the fish angular velocity decreased (72±20, 145±32 and 32±210 degrees.s^{-1} for *Wild*, *Domesticated* and *Selected* fish respectively) but stayed at a higher level than during S1 ($F_{2,120}$=22.01, p<0.0001; Fig.5). For each sequence, *Selected* fish changed direction slower than *Wild* and *Domesticated* fish, which were not different ($F_{2,120}$=11.15, p<0.0001; Fig.5). There was no significant interaction between sequence and strain factors ($F_{4,120}$=2.47, p>0.05) which again underlined an homogeneity in strains responses to the standardized stressor.

4. Discussion

4.1. Basic locomotory activity

The spatial exploration behaviour is generally considered as a good indicator of an animal adaptation to its environment. Indeed, such behaviour contributes to the construction of cognitive maps based on the coupling of space elements in which the animal moves (O'Keefe and Nadel, 1978). The capacities to explore an open field (potentially dangerous) could also depend on the animal personality (bold or shy). Indeed, for Fraser et al. (2001) and Wilson et al. (1993, 1994) boldness is considered as a personality trait and is generally defined as the propensity to take risks.

According to our first results, it appeared that each strain presented different exploration behaviour and thus different environmental adaptation capacities, and the proportion of bold and shy fish was also different. Indeed, 64% of *Selected* fish had been stimulated after only 9 min and they also showed a higher distance travelled in the tank and a lower swimming path complexity during the first experimental period compared to the other strains. Thus, S*elected* fish seemed characterized since the beginning of the experiment by a better environmental adaptation and a bolder personality than the other strains.

4.2. Flight response and evolution of fish exploration behaviour

Blanchard et al. (1986, 1989) showed in mice that two major systems of defense behaviour existed. The first system could be observed when a threatening stimulus was physically present and identifiable. This system which aims to reduce danger exposure toward threatening stimulus, involves

flight or escape behaviour, which are typical of fear responses. The second system could be observed during potential threatening situation when the stimulus was not clearly identifiable. This case corresponded to a situation in which animals were previously frightened by the stimulus. They presented then, three types of behaviour: avoidance of danger area, risk assessment (to evaluate and to locate) and thigmotaxis (tendency to remain close to the walls of an open field). These two major systems of defense were also observed in sea bass from the three strains tested during this experiment which mainly displayed both flight response and thigmotaxis. First, observations and video-tracking analysis showed that the stimulation induced for all fish a flight response in the opposite direction from the stimulus impact zone as illustrated by the significant increase of time spent in zone 4. This zone could thus be defined as a "refuge" zone in which fish were characterized by a freezing behaviour, *i.e.* reduced swimming activity along the walls or total motionlessness. These results were in accordance with other studies realized on *Dicentrarchus labrax* (Malavasi et al., 2004, 2008), on *Oncorhynchus kisutch* (Ryer, 2004), on *Calidris alpina* (Barbosa, 1997), on *Salmo trutta* (Fernö and Järvi, 1998), on *Salmo salar* (Gotceitas and Godin, 1991), and on two species of stickleback *Gasterosteus aculeatus* and *Pungitius pungitius* (Godin and Valdron Clark, 1996). Such common flight response toward a threatening stimulus observed for all fish species, and for all strains in our case study, suggests that such behaviour has a strong innate determinant (Giles, 1984; Vilhunen and Hirvonen, 2003), could not be influenced by domestication and selection level and could thus be considered as a fundamental component of anti-predator behaviour.

Second, swimming activity and spatial exploration seemed strongly impaired by the stimulation and characterized by the second system of defense highlighted by Blanchard et al. (1986, 1989). The significant higher residency in zone 4, the decrease of distance travelled, the increase of swimming complexity and the thigmotaxis behaviour in zone 4 were thus all typical indicators of fish avoidance of a dangerous area and of risk assessment. Forty minutes after the stimulation, fish recovered a higher level of spatial exploration and swimming activity *i.e.* fish globally showed a decreased residency in zone 4, an increase of distance travelled in the tank and a decrease in swimming complexity. These informations seemed to show that fish were less affected than just after the stimulation and began to recover homogeneous swimming activity in the tank. However, the levels of each variable did not

return to the previous ones observed before stimulation, which indicated that fish remained fearful toward the stimulus.

Even if the general behavioural reaction of fish was the same in the three strains, *Selected* fish were still characterized by a higher swimming activity and a lower path complexity than other strains whatever the experimental sequences. Thus we could not conclude that *Selected* fish were differentially affected by stimulation than the other strains, but they were characterized since the beginning by a better environmental adaptation and a bolder personality which was kept during the entire test.

Malavasi et al. (2004, 2008) showed that hatchery-reared fish were characterized by a shorter stress response to threatening stimulation than fish of wild origin. In our experiment *Wild* and *Domesticated* fish presented the same spatial exploration behaviour and the same swimming activity. Therefore and since our *Wild* fish were not caught in the sea but issued from wild caught parents, our results could suggest that a twenty months period of rearing (first generation fish) could be sufficient to obtain fish presenting the same behavioural characteristics than second generation fish.

The behaviour and personality differences observed between *Selected* fish and the other fish strains in our experiment could not be explained by behavioural deficits in anti-predator behaviour incurred through rearing in a psychosensory-deprived environment (Olla et al., 1994) or by the lack of some key experiences in early life stage (Huntingford, 2004; Kelley and Maguran, 2003; Price, 1999), because all of our fish were hatchery born and reared under the same conditions. Moreover, the experiment was done on fish with similar weight for the three strains in order to limit any size influence on behaviour since some studies have demonstrated that fish selected for their high growth showed an increased willingness to accept risk (Biro et al., 2004; Fernö and Järvi, 1998; Huntingford and Adams, 2005; Johnsson and Abrahms, 1991; Johnsson et al., 1996). Thus, the difference observed in our study could only be explained by the selection for growth process. We could then suggest that parent selected for growth (and thus perhaps characterised by a better adaptation to rearing environment) transmit this ability to their descendents.

In conclusion, the present study has demonstrated that wild fish (*i.e. Wild* strain which was issued from wild parents with at least on year in captivity) behave similarly to the domestic fish (*i.e. Domesticated* strain). Further, selection for growth seemed to select fish characterized by a bolder personality and potentially better adapted to rearing environment. Thus, selection for growth seemed to have a higher effect on fish personality and behaviour than domestication only. Nevertheless, to test the perpetuation of domestication and/or selection effects on sea bass behaviour, personality and adaptability, it would be necessary to perform measurement on fish issued from following generations of domestication or selection.

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Figure captions

Figure 1. (**A**) Representative scheme of the experimental set up to a scale of 1/20 and (**B**) the zones delimitation on the tank bottom to a scale of 1/10.

Figure 2. Representative pictures of one fish swimming behavior for each of the 3 sequences in correspondence with the experimental time scale.

Figure 3. Proportion of time spent (mean ± SE, in %) by a fish in each tank zone for each sequence and for each strain.

Figure 4. Distance travelled (mean ± SE in cm) by a fish in the tank for each sequence and for each strain. Letters indicate significant differences between strains (2 fixed factors ANOVA and Newman & Keuls test, $p<0,05$).

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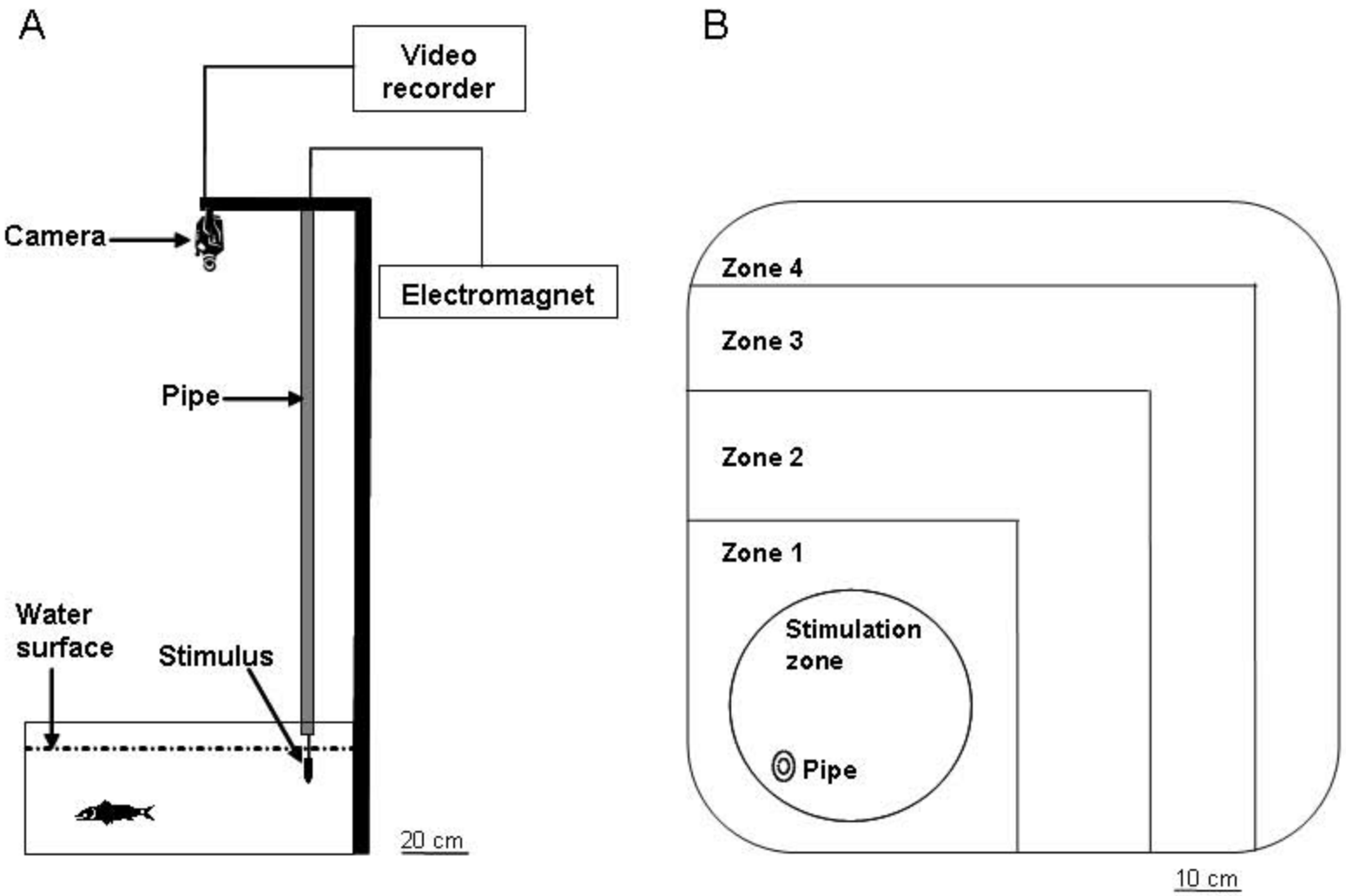
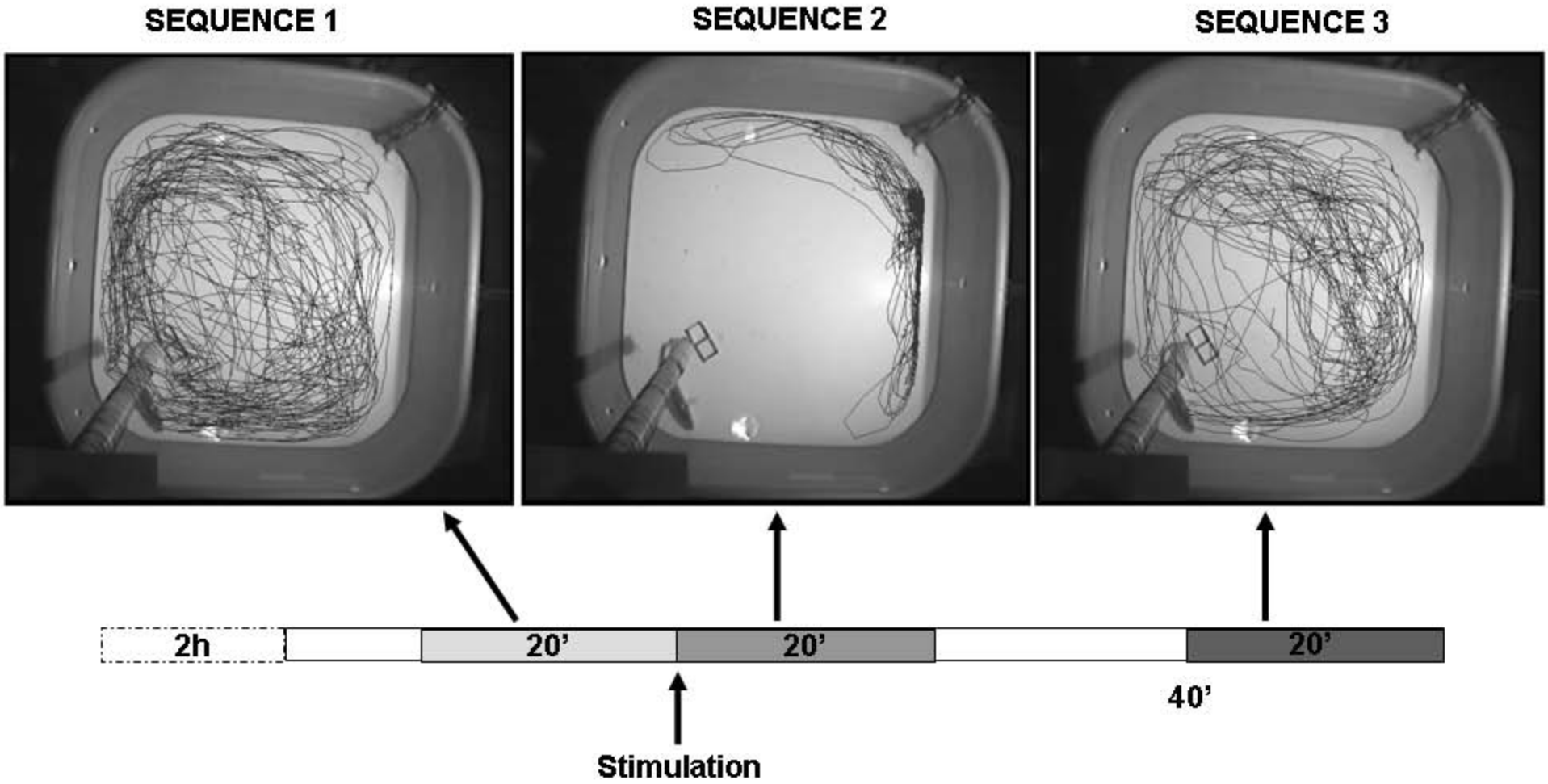
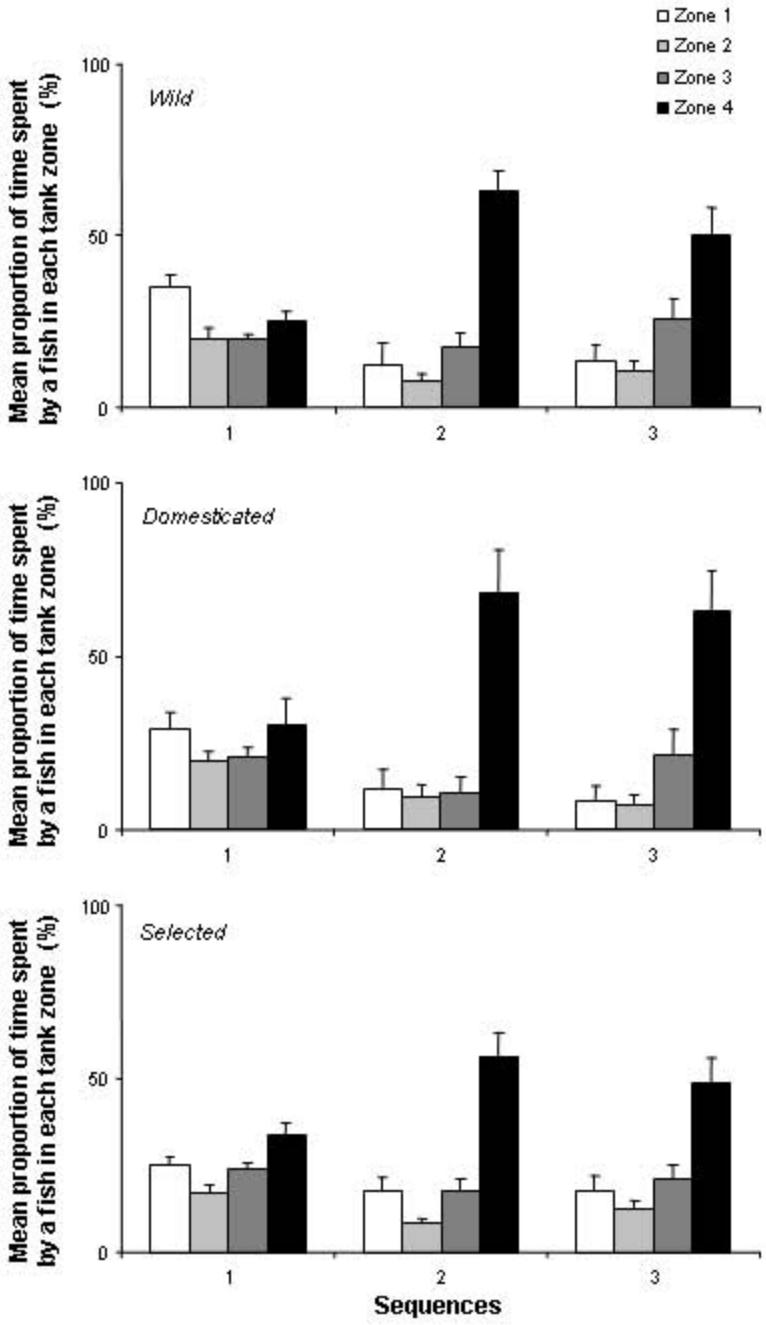
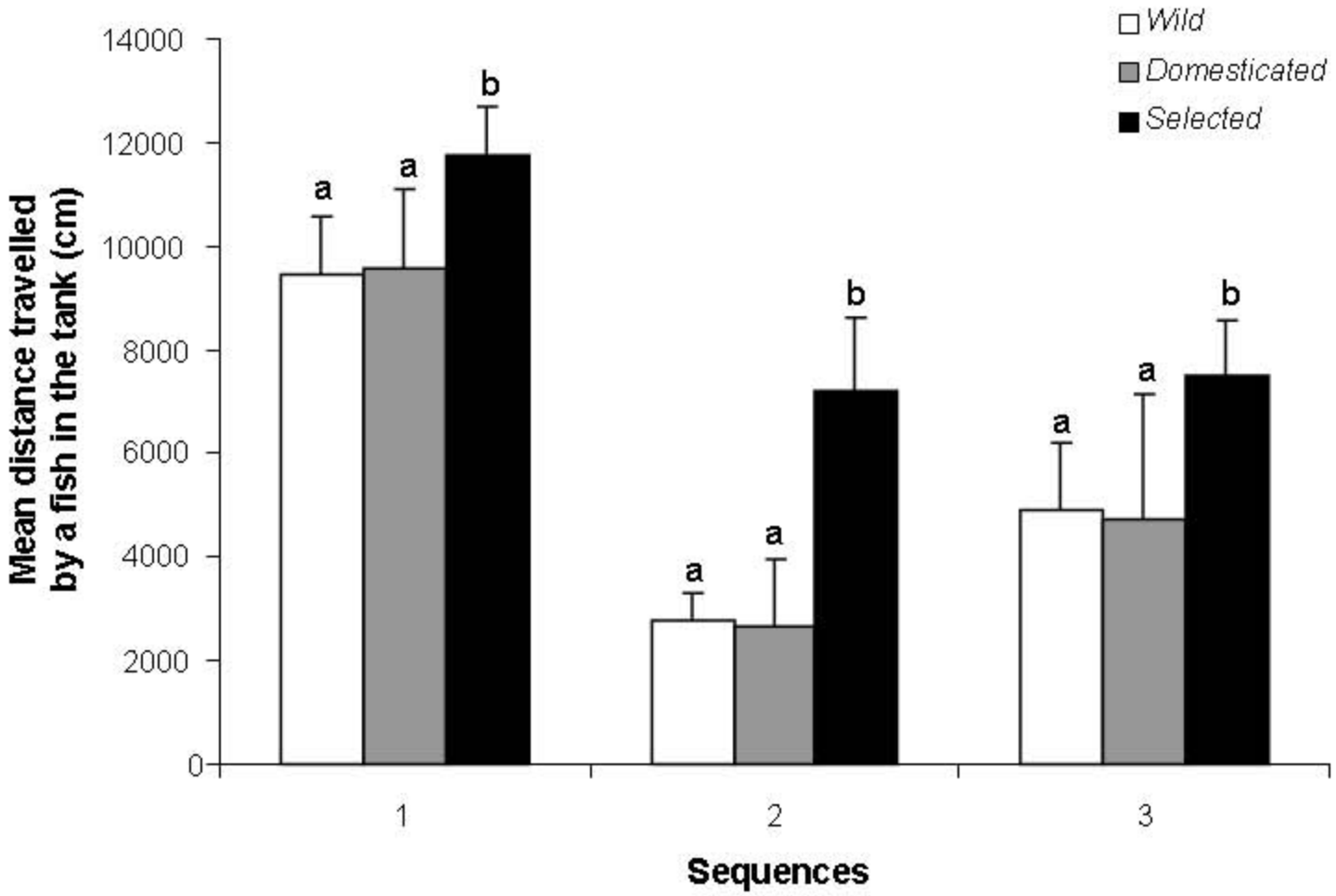
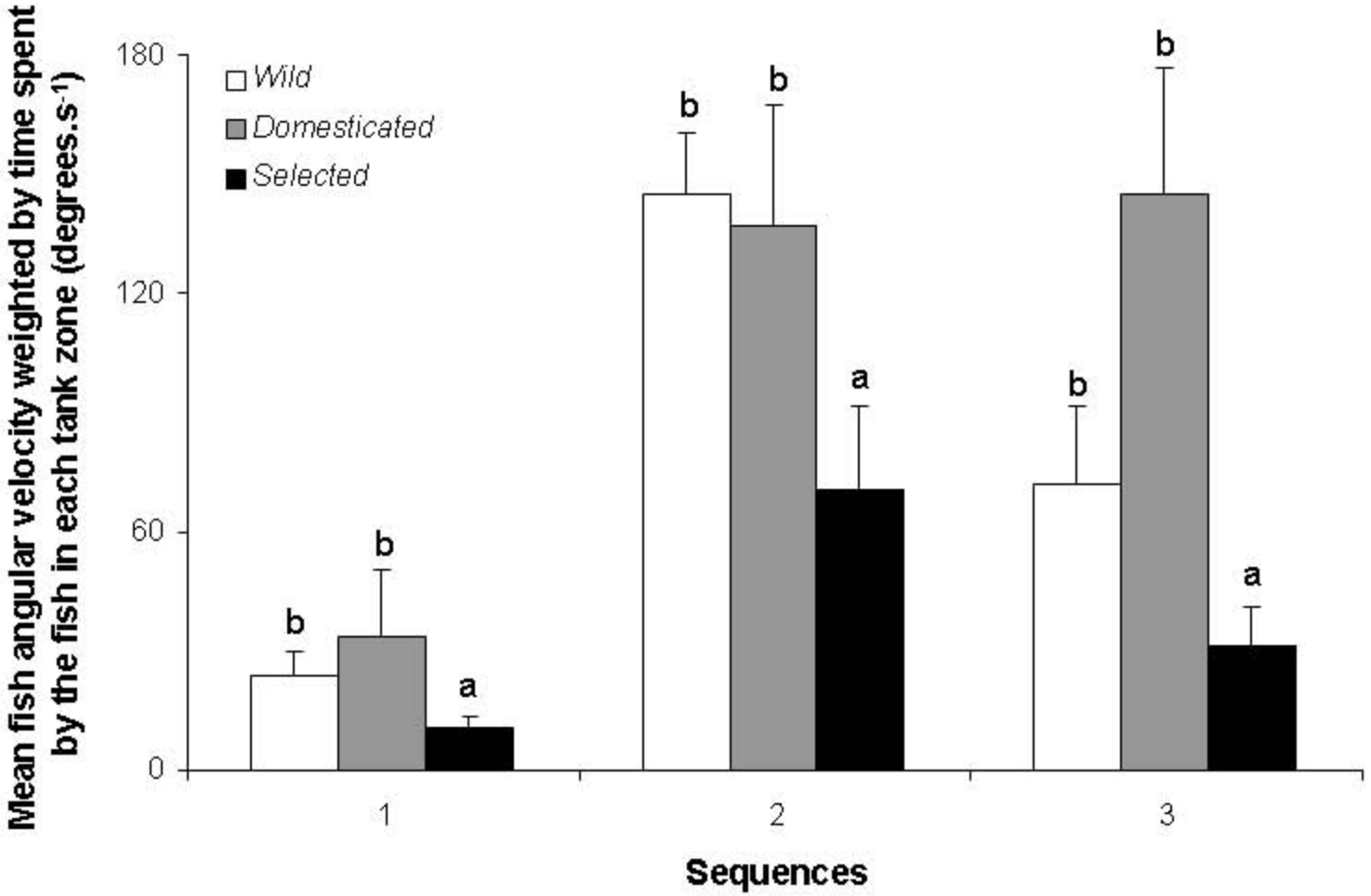
Figure 5. Fish angular velocity weighted by the time spent by the fish in each tank zone (mean ± SE in degrees.s^{-1}) for each sequence and for each strain. Letters indicate significant differences between strains (2 fixed factors ANOVA and Newman & Keuls test, $p<0,05$).


A
Video recorder
Camera
Electromagnet
Pipe
Water surface
Stimulus
20 cm
B
Zone 4
Zone 3
Zone 2
Zone 1
Stimulation zone
Pipe
10 cm


SEQUENCE 1
SEQUENCE 2
SEQUENCE 3
2h
20'
20'
20'
40'
Stimulation


Zone 1
Zone 2
Zone 3
Zone 4
Wild
Domesticated
Selected
Mean proportion of time spent by a fish in each tank zone (%)
100
50
0
1
2
3
Sequences


Wild
Domesticated
Selected
Mean distance travelled by a fish in the tank (cm)
14000
12000
10000
8000
6000
4000
2000
0
a
a
b
a
a
b
a
a
b
1
2
3
Sequences


Mean fish angular velocity weighted by time spent by the fish in each tank zone (degrees.s-1)
180
120
60
0
Wild
Domesticated
Selected
b
b
a
b
b
a
b
b
a
1
2
3
Sequences