Food deprivation reduces social interest in the European sea bass *Dicentrarchus labrax*

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SUMMARY STATEMENT

This article describes the effects of food-deprivation upon three behavioural traits risk-taking, exploratory activity and solitariness, as well as the relationship between them, in juvenile sea bass.

ABSTRACT

Periods of food deprivation up to several months are common features for fishes and in such conditions, fitness will be determined by their capacity to maximize food encounter while minimizing predation risk. In this context, the propensity to take risk and the willingness to associate with conspecifics are particularly important as they contribute to alleviating the trade-off between predation avoidance and foraging efficiency. This study examined to what extent food deprivation modulates fish risk-taking and social behaviours, as well as the relationship between them. To address these issues juvenile European sea bass were either fed daily with a maintenance ration or food-deprived during 3 weeks. Risk-taking and sociability were assessed through measurements of fish willingness to explore a novel environment, to interact with a novel object or a conspecific. Multivariate analysis allowed the identification of three behaviours, risk-taking, exploratory activity and solitariness. Food-deprived fish interacted less with conspecifics than control fish. After food-deprivation, no difference in terms of risk-taking and exploratory patterns was observed. Finally, the relationship between risky-taking and solitariness was influenced by the feeding status. When food-deprived fish with higher propensity to take risk displayed increased solitariness while, when fed normally they interacted more with conspecifics.

INTRODUCTION

Food availability and accessibility are key determinants of fitness (Patrick et al., 2017). In aquatic ecosystems, finding and capturing prey are uncertain and periods of starvation up to several months are not unusual (Gingerich et al., 2010). In such conditions, animals preserve their fitness through behavioural responses which maximize food encounter and capture rates while minimizing predation risk (Lima and Dill, 1990). When food is scarce, increasing the duration and extent of food searching, further away from a shelter for instance, is a risk-prone behaviour which favours food encounter. The drawback of such behaviour is increased predator encounter rate and, therefore, increased mortality risk (Biro and Stamps, 2010; Lima and Dill, 1990). In contrast, risk-averse behaviours such as staying in a protective area, benefits the individual through energy saving and reduced predation risk. The downside of this strategy is obviously a reduction in feeding opportunities (Krause and Ruxton, 2002).

Risk taking has major consequences for individual's fitness as it has been shown to correlate with growth, energy metabolism, dispersal, breeding success, offspring nourishing and social dominance (Ariyomo and Watt, 2012; Bell and Sih, 2007; Brown et al., 2005; Cote et al., 2010; Dingemanse et al., 2004; Greenberg and Mettke-Hofmann, 2001; Huntingford et al., 2010; Jolles et al., 2015; Mutzel et al., 2013; Rudin and Briffa, 2012). Risk-prone individuals accept higher risk in return for gaining information and possibly increased reward. Risk-averse individuals, on the other hand, tend to avoid potentially risky situation, accepting reduced gains in return for lower risk. It should however be recalled that willingness of one individual to take risk is context dependent (Coleman and Wilson, 1998). For instance, Galhardo et al. (2012) showed that social context influences risk-taking of male cichlid fish (*Oreochromis mossambicus*), fish in the presence of familiar conspecific being more prone to accept risk than fish in the presence of unfamiliar conspecific or in social isolation. This context-dependency of risk-taking is the cause of disagreement among authors regarding the most appropriate methodology to assess it (Carter et al., 2013; Conrad et al., 2011; Réale et al., 2007; Wilson et al., 1993). While some authors restrict the measures of risk acceptance to the context of predation (Réale et al., 2007), other authors extend the relevance of the notion to any context where an animal has to make a decision toward unfamiliar and potentially dangerous stimuli (Frost et al., 2013; Leblond and Reebs, 2006; Nakayama et al., 2012; Toms et al., 2010; Wilson et al., 1993). In the present study, risk-taking is

considered in its broader sense, with exploratory tendency and neophilia been recognised as components of individuals' willingness to take risk.

Sociability is an important modulator of fish behavioural responses to the environmental context and, particularly, of the trade-off between maximizing foraging opportunities and minimizing predator encounter. Sociability is classically defined as one animal's reaction to conspecifics, apart from aggressive interactions (Conrad et al., 2011). Fish express sociability in species specific manners one of which is the willingness to shoal. Shoaling behaviour is considered as a flexible strategy by which individuals increase food detection while lowering predation risk through additive vigilance, numerical risk dilution and predator confusion effect (Clark and Mangel, 1986; Godin, 1986; Krause and Ruxton, 2002; Krause et al., 2000a; Pitcher and K. Parrish, 1993; Pulliam and Caraco, 1984). Shoaling is, however, also associated with increased competition within the group (Pitcher, 1986; Pulliam and Caraco, 1984). Shoal formation relies on the decisions of individuals to remain together and it has been proposed that food restriction influences individual decision regarding self-assembly with conspecifics (Frommen et al., 2007; Raubenheimer et al., 2012). For instance, Krause (1993), Barber et al. (1995) and Hensor et al. (2003) reported that food-deprived fish tended to spend more time alone than well-fed individuals. However, at least one study described the reverse response (Killen et al., 2016). Sociability characterizes animals' inclination for social interaction such as shoaling. In the present study, solitariness is used as the reciprocal of sociability, high solitariness reflecting individuals' unwillingness to group with conspecific, while low solitariness indicated individual inclination for social interaction.

Analysing behaviours is a key component in understanding how fish populations respond to seasonal and stochastic variations in environmental conditions. Equally important is the interaction between those behaviours. The relationship between risk-taking and sociability has been examined in fish, and whereas a relationship was found in some species (*Symphodus ocellatus*, Budaev, 1997; *Gasterosteus aculeatus*, Ward et al., 2004), it was not observed in others (*Danio rerio*, Moretz et al., 2007). Moreover, when found, this relationship displayed different shapes depending on the species considered. In most species examined, a negative correlation between risk-taking and sociability has been reported (*Symphodus ocellatus*, Budaev,

1997; *Gasterosteus aculeatus*, Ward et al., 2004; Harcourt et al., 2009; *Lepomis gibbosus*, Wilson et al., 1993). In the mosquitofish (*Gambusia affinis*, Cote et al., 2010) as well as in two terrestrial ectotherms, the red ants (*Myrmica spp.*, Chapman et al., 2011) and the European green lizard (*Lacerta vivipara*, Cote & Clobert, 2007), the reverse was observed, with a positive correlation between risk-taking and sociability. It has been proposed that correlation among behaviours might be adaptive as they contribute to individual fitness (Bell, 2005; Bell and Sih, 2007; Bell and Stamps, 2004). In the three-spined sticklebacks, for example, no interaction between risk-taking (swimming activity after a predator attack) and aggressiveness (toward conspecifics) was observed under low predation pressure. Under the high predation pressure, however, a positive correlation between these behaviours was observed (Bell, 2005). Although disappointing, these conflicting results may not be all that surprising as there is no reason why relationships between behaviours should all have the same shape across vastly different experimental systems using species with different ecologies and behavioural repertoires. Thus, to better assess the true adaptive value of fish behavioural strategies, future studies should the relationships between behavioural traits with particular consideration for the strength and shape of these relationships.

Using juvenile European sea bass (*Dicentrarchus labrax* Linnaeus 1758) as a model species, the present study investigated to what extent food deprivation modulates fish risk-taking and social behaviours, as well as the relationship between them. At juvenile stage, European sea bass form shoals that occupy shallow costal habitats were spatial and seasonal fluctuations in prey availability are common, exposing them to periods of starvation (Claireaux et al., 2013; Dupont-Prinet et al., 2010). Four commonly used behavioural tests were implemented, with the initial anticipation that they would allow assessing risk-taking and sociability through the measuring of the willingness of individuals to explore a novel environment, to interact with a novel object or a conspecific and to use a shelter. Behavioural responses of 3 weeks-food deprived fish were compared to those of control individuals fed daily with a maintenance ration. Three hypotheses were tested (1) starvation favours solitariness to avoid competition for food, (2) starvation increases risk-taking and exploratory activity to enhance food encounter and (3) food-deprivation modulates the relationships between solitariness, exploratory activity and risk-taking.

MATERIALS AND METHODS

Study animals

Fifty-six juvenile European sea bass *Dicentrarchus labrax* Linneaus 1958 (age 0^+, mass=14.6±0.08 g, mean±Standard error of the mean) were obtained from a local fish farm (Aquastream, Lorient, France). Upon arrival to the laboratory (Ifremer, Brest, France), fish were anesthetized (MS-222; 20 mg L^{-1}), measured for total length and mass and implanted subcutaneously with an identification tag (RFID; Biolog-id, France). Fish were then placed in a 2000-L indoor tank supplied with open flow, thermoregulated (20°C) and fully aerated sea water, salinity of 32 ppt. Artificial lighting followed local photoperiod. Fish were fed daily with a maintenance ration (1% body mass) using commercial feed (Neo Start Coul 2, Le Gouessant, France). The experiments were approved by the French Ethics Committee in charge of Animal Experimentation n°74 (permit number: APAFIS#3814-2016012715396101 v2) and were in accordance with institutional guidelines. The experimental procedures were noninvasive.

Experimental protocol

Fish were acclimated to the laboratory conditions during two months before the following procedure was implemented. On an alternate week basis a set of eight fish was randomly selected from the holding tank, anesthetized (MS-222; 20 mg L^{-1}), measured for total length and mass and transferred to one of two treatment tanks (50 L). These treatment tanks were situated in the experimental room and received the same water and light conditions than the original holding tank. The two experimental treatments were a control treatment (C), where fish were fed normally, and a food-deprived treatment (FD), where fish were not fed during a 3-week period.

Following the 3-week of either C or FD feeding treatment, a set of 8 fish from one experimental treatment tank was submitted to the following protocol (Fig. S1). Fish were gently placed (without emersion) into one of eight individual confinement chambers. These chambers consisted of an opaque PVC tube (13 cm×5 cm length, diameter respectively) closed at both end with plastic meshing to allow water renewal inside the chamber. These chambers were then placed side by side on the bottom of a recovery tank and fish were left undisturbed for an additional 24 h. The 8 fish were then successively submitted to a sequence of four consecutive trials which spanned over 4 days. On each testing day, the running order of the 8 fish was randomized. Using

a 2 L plastic container filled with water, each chamber was smoothly moved from the recovery tank to the experimental arena. After 3 minutes to recover from potential disturbance arising from the transfer, one end of the tube was opened from a distance and the fish allowed 1 min to exit the chamber. In most cases (49 over 56), the tube had to be gently lifted to encourage the fish to swim out. Following their entrance in the arena, nearly all fish displayed a period of agitation which typically lasted less than a minute. To avoid including this "flight response" in our analysis, the first minute following fish entry in the testing arena was not taken into consideration during video analysis.

The testing arena consisted of a white rectangular shallow tank (156 cm×99 cm×14 cm, length, width, height, respectively). A curtain placed around and over the arena screened fish from visual disturbance. The arena was filled with the same water than the rearing and treatment tanks and was homogeneously lighted (30 lux) using neon lamps.

A camera (Logitech webcam C930e) situated 1 m above the water surface allowed the recording (15 frames s^{-1}) of fish movements during the 30 minutes that followed fish entry into the arena. Following the 30 min trial, the tested fish was returned to its PVC tube which was then placed back into a new recovery tank until the next day. This recovery tank allowed separating already tested fish from those waiting to be tested, preventing the transfer of chemical cues between fishes. Water conditions in recovery tanks were identical than in the treatment tank. Once a fish had been removed from the arena it was emptied, refilled and the next fish was brought in.

Experimental sets of fish were successively submitted to the following sequence. The first day, fish were submitted to a novel environment test which consisted in exposing fish to a bare tank. The second day, a novel object was placed at the centre of the arena prior the introduction of the fish. The object consisted of a white, opaque polypropylene jar (13 cm height, 10.5 cm in diameter) with holes (1.5 mm) all around. The object was placed in such a way that no shadow was created in the arena. The third day, a conspecific was placed in the opaque jar and 20 minutes later the tested fish was transferred in the arena. The conspecific was placed inside the perforated jar allowing transfer of chemical cues and pressure waves in relation with movement but preventing visual contact with the focal fish and the establishment of dominant-subordinate

relationships. Finally, the fourth day a refuge, which consisted of a flat piece of black plastic (19 cm × 19 cm, length, width, respectively), was placed on the bottom in one corner of the arena, opposite from the fish release site (Nelson and Claireaux, 2005). This fixed temporal order of the four assays allowed keeping the same potential carry-over effects between trials carried out on successive days. In addition, this order was established to familiarize the fish to one condition before testing the following one, introducing only one change in each test. The first assay allowed the fish to familiarize with the arena which was then no longer considered as a novelty at day 2. Day 2 the Novel object was added as the only source of novelty in the familiar arena. Day 3, the fish was already familiar with this object and it allowed evaluating interest for a conspecific by adding a non-focal fish inside the object. This individual was used as a social stimulus for the whole day (8 trials). It was taken from the holding tank and was placed inside the polypropylene jar 20 minutes prior to the beginning of the experiment. Finally, day 4 refuging behaviour was tested by evaluating fish capacity to localise and use a refuge in an already well explored arena. At the end of the week, the 8 fish were anesthetized (MS-222; 20 mg L^{-1}) and their total length and body mass measured to estimates specific growth rate. They were then returned to their original holding tank.

Behavioural analyses

During day 1, four indices of activity were measured during the first 5 minutes of the test (i.e. the total time spent swimming, TSwim; the number of sections crossed, NbSC; the time spent in the central section of the arena, TCent; and the number of entries in the central section, NbECent). To score NbSC, a grid was placed over the screen of the computer used for video analysis. This grid divided the arena in 16 sections of equal dimensions (39 cm×24.75 cm) whereas to score TCent, the central section (78 cm×49.5 cm) was distinguished from the periphery of the arena. Analysing day 2 consisted in measuring, during the first 5 minutes period of the test, four new indices of activity (i.e. the latency before the first approach to the novel object, LatNO; the time spent close to the novel object, TNO; the number of approaches to the novel object, NbApproachNO; and the number of revolution around the novel object, NbRevNO). In this test, the fish was considered close to the conspecific when it was less than a body length away from it. During day 3, the variables of interaction with the conspecific were measured during the last 5 minutes of the 30 minutes test to ensure that the focal fish detected the conspecific. During this

test, the same four variables as during day 2 were measured (i.e. the latency to approach the conspecific, LatConsp; the time spent close to it, TConsp; the number of approaches, NbApproachConsp; and the number of revolution around, NbRevConsp). Again, the fish was considered close to the object with the conspecific when it was less than a body length away from it. Finally, analysing day 4 consisted in recording the following three indices over the 30 minutes of the test (i.e. the latency to enter in the shelter, LatShelt; the time spent in the shelter, TShelt; and the number of exit from the shelter, NbOutShelt). Note that the same observer scored the different behaviours by visual observation from the videos.

Statistical analysis

Due to video failure, two fish were excluded from the analyses.

Owing to our experimental design, one possible analytical option was to analyze each test separately, as in Dingemanse et al. (2010) for example. We opted for a more integrative approach using a principal component analysis (PCA) that regrouped, on the same axes, the variables that assessed a common behaviour. Three principal components (PCs) were chosen according to Kaiser's criterion (Kaiser, 1961), retaining only factors with eigenvalues greater than 1. Linear combination of the variables was used to label the 3 PCs, *Risk-taking* (PC1), *Exploratory activity* (PC2) and *Solitariness* (PC3), respectively. Behavioural scores of FD and C fish were compared using parametric multivariate analysis of variance (MANOVA), followed by ANOVA tests to generate univariate statistics. A linear model was fitted to compare the relationship between Risk-taking and Sociability in C and FD fish. In this model, feeding treatment, Risk-taking (PC1) and Exploratory activity (PC2) including the interactions treatment×(PC1+PC2), were used as explanatory factors influencing the Sociability (PC3) which was used as the response variable. A backward stepwise reduction of the full model was then applied to exclude non-significant interactions.

All statistical analyses were performed using R version 3.3.1(R Development Core Team, 2006) with package FactoMineR (function PCA) with all variables scaled and package stats (functions manova, summary.aov and lm). Model diagnostics were evaluated using graphical procedure (Q–Q plot). Statistical significance was accepted at $P<0.05$.

RESULTS

Data were collected from *N*=30 control (C) and *N*=23 food-deprived (FD) fish. Mean initial mass was 14.6±0.10 g and 14.5 ± 0.16 g for the C and FD fish respectively. Mean specific growth rates measured over the 3-week treatment period was 0.9±0.07% day^{-1} and -0.3±0.03% day^{-1} for the C and FD fish respectively.

Reduction and structure of the variables

The impact of starvation on the behaviour of juvenile sea bass was analysed using two successive principal component analyses (PCA). The first PCA included the 15 variables extracted from the novel environment (day 1), novel object (day 2), conspecific (day 3) and shelter (day 4) experimental trials. The variables whose contribution to the construction of the PCA axes was lower than the mean contribution of the 15 variables initially tested were then removed and a second PCA was conducted (Cibois, 1986; Cibois, 1997). In this process, the three variables measured during the shelter trial (day 4) were excluded. Moreover, one individual with a contribution to the structure of the axes twenty times higher than the median contribution of all the individuals was considered as an outlier and removed from the analysis. In this second PCA, three principal components were selected (eigenvalue>1) which represented 75.15% of the total variance in our data set (Table 1). The three principal components were respectively interpreted as indicators of *Risk-taking, Exploratory activity* and *Solitariness*. This labelling resulted from the specific linear combination of variables on each axis. Principal components are described in the following paragraphs.

The first principal component (PC1) explained 34.64% of the variability. This axis was labelled *Risk-taking* as it incorporated eight variables measuring fish propensity to take risk when exposed to novelty. These included the three variables measuring the interaction with the novel object (day 2: time spent close to the novel object, TNO; number of approaches to the novel object, NbApproachNO; number of revolution around the novel object, NbRevNO) and the three variables measuring the interaction with the newly introduced conspecific into the familiar object (day 3: time spent close to the conspecific, TConsp; number of approaches to the conspecific, NbApproachConsp; number of revolution around the conspecific, NbRevConsp). Also included here are the two variables measuring the latency before the first approach to the novel object

(LatNO) and to the conspecific (LatConsp). The former six variables correlated positively with the first principal component while the latter two correlated negatively with PC1 (Table 2). On PC1, positives scores indicated risk-prone individuals, while negative scores indicated risk-averse individuals.

The second principal component (PC2) explained 25.40% of the total variance. This axis was labelled *Exploratory activity* as it was defined by four variables measuring fish activity during the discovering of the novel environment day 1 (i.e. total time spent swimming, TSwim; number of sections crossed, NbSC; time spent in the central section of the arena, TCent; and number of entries in the central section, NbECent). These four variables correlated positively for this axis (Table 2). On PC2, individuals with higher exploratory tendency had positive scores, while less exploratory individuals had negative scores.

The third principal component (PC3) explained 15.11% of the variability. This axis was labelled *Solitariness* as it was defined by two sets of variables that distinguished interaction with the empty object (day 2) from interaction with the object in the presence of a conspecific inside that object (day 3). The first set of variables included TNO, NbApproachNO and NbRevNO and it correlated positively with PC3. The second set included TConsp, NbApproachConsp and NbRevConsp and it correlated negatively with PC3 (Table 2). On this third principal component, solitary individuals had positive scores, while individuals with more social interest displayed negative scores. It is important to point out, however, that these variables also loaded heavily on PC1. This third principal component should therefore be interpreted with caution. Nevertheless, it allowed us to explore fish social behaviour by differentiating interaction with the empty object from interaction with a conspecific inside this object.

To summarize, when transferred in the experimental arena, fish that scored high on PC1 took less time to make the first approach to the object in the centre (day 2 and day 3; low LatNO and LatConsp) and spent more time at close distance from it (day 2 and day 3; elevated TNO, NbApproachNO, NbRevNO, TConsp, NbApproachConsp and NbRevConsp) (Fig. 1A, B, C, D). On the other hand, fish that scored high on PC2 spent less time motionless (elevated TSwim), moved greater distances (elevated NbSC) and explored more actively the central zone of the

arena (elevated TCent and NbECent) (Fig. 1A, B, E, F). Finally, fish that scored high on PC3 were more in contact with the object when it represented a novelty (day 2; elevated TNO, NbApproachNO and NbRevNO) but had minimal interaction with the central object in the presence of a conspecific inside (day 3; low TConsp, NbApproachConsp and NbRevConsp) (Fig. 1C, D, E, F).

Effects of the feeding regime

Multivariate analysis of variance showed that, overall, the effect of the feeding regimes on fish behaviour was significant (*Pillai's Trace*=0.242, $F_{1, 49}$=5.202, P=0.003). Going into the detail, fish from the two feeding regimes showed no statistically different scores on PC1, (Fig. 1B, D; *Risk-taking,* $F_{1, 51}$=0.678, P=0.414). However, they showed nearly statistically different scores on PC2, the significance threshold being almost attained (Fig. 1B, F; *Exploratory activity,* $F_{1, 51}$=3.784, P=0.057). Finally, the two feeding treatments yielded statistically different scores on PC3 (Fig. 1D, F; *Solitariness*, $F_{1, 51}$=9.670, P=0.003), food-deprived (FD) fish displaying higher scores than control (C) fish, meaning that food-deprived fish interacted less with the conspecific than well-fed fish.

Factors influencing solitariness

Individual degree of risk-taking was expected to influence social behaviour. This relationship was investigated using a linear modelling approach (Table 3). The resulting model indicated that PC3 (*Solitariness*) was influenced by PC1 (*Risk-taking*) differently according to the feeding treatment ($F_{4, 48}$=5.423; Treatment×PC1 *Risk-taking* interaction, P=0.003; Table 3). Figure 2 illustrates the different correlations between scores on PC1 and PC3 according to the feeding treatment. These scores correlated positively for FD fish (P=0.022), while they displayed a nearly significant negative correlation in C fish (P=0.064). Despite these differences between feeding treatment groups, it should be noted that at the left end of PC1 (risk-averse individuals) fish were undistinguishable from one another with regard to their social interest (PC3). However, individuals' solitariness level progressively differentiated according to their feeding regime has their scores on PC1 increased (Fig. 2).

DISCUSSION

The aim of the present study was to examine to what extent sea bass nutritional status modulates risk-taking and sociability. Three hypotheses were tested: (1) starvation favours solitariness to reduce competition for food, (2) starvation increases exploratory activity and risk-taking to enhance food encounter and (3) food-deprivation modulates the relationships between solitariness, exploratory activity and risk-taking. In accordance with our first hypothesis, food-deprivation modulated the interaction with conspecific, food-deprived (FD) fish interacting less with conspecifics than control (C) fish. However, contrary to our second hypothesis, C and FD fish did not differ in terms of risk-taking and exploratory patterns. In agreement with our third hypothesis, we observed that feeding status influenced the relationship between risk-taking and solitariness, risk-prone fish displaying increased solitariness when food restricted and reduced solitariness when fed normally.

Behaviours

Using principal component analysis (PCA), the impact of feeding status on fish response to novelty was explored. Through this approach, the fifteen measured variables were combined into smaller sets of interpretable linear combinations (components). Three components were identified which explained 75% of the variability of fish behavioural patterns. The first component was considered to indicate *Risk-taking* as it included variables usually attributed to the propensity to take risk when faced with novelty. The second component of our PCA was termed *Exploratory activity* as it informed about fish swimming activity level and pattern while explorating of a novel environment. The third component was considered to specify fish level of *Solitariness* as it was defined by measures of individuals' unwillingness to group with conspecific.

Due to terminological and methodological inconsistencies, the delineation of behaviours can be somewhat subjective, potentially resulting in conflicting interpretations (Carter et al., 2013; Roche et al., 2016; Toms et al., 2010). The current data set provides a new illustration of the difficulty of contextually interpreting and labelling behavioural responses. The exploration of the central zone in a novel environment test as well as the response to a novel object during the novel object test, are classically used to assess one individual's degree of risk taking in response to novelty (Boulton et al., 2014; Budaev, 1997; Burns, 2008; Frost et al., 2013; Sneddon, 2003;

Wilson et al., 1993; Wright et al., 2003). In the present study, however, variables issued from these two tests did not correlate with each other, indicating that they may not evaluate the same behaviour. Whereas variables from the Novel Object test correlated on PC1, the number of entries and the duration of the stays in the central zone correlated with the total time spent swimming and the number of sections crossed in the Novel Environment test on PC2. This linear combination on PC2 supports the hypothesis that the number of entries and the time spent in the central zone may simply be proportional to individuals' activity level, with more active fish passing more often and spending more time in the centre of the experimental arena than less active fish. We suggest that those four variables are indicators of *Exploratory activity* level rather than indicators of risk-taking.

One major requirement to define one animal's personality trait is that the inter-individual differences in the corresponding behavioural measure must be consistent. However demonstrating consistency implies that the measure is repeated several times in exactly the same context. In the present experiment this was clearly not the case, fish behaviours were measured only once. Consistent with the fact that the repeatability of fish responses was not evaluated, we considered that the tests used in the present study evaluated the impact of starvation on behavioural tendencies (risk-taking, exploratory activity and solitariness) and not on personality traits (boldness-shyness, exploration-avoidance, sociable-associable).

Effect of food-deprivation
The effect of a three-week food-deprivation period on solitariness, risk-taking and exploratory activity was evaluated. In line with our first hypothesis, starvation favoured solitariness in sea bass. Conflicting with our second hypothesis, however, food-deprivation had no impact on risk-taking and exploratory level.

It is important to emphasize that the third component of our PCA, *Solitariness*, explained only 15% of variance in our data set, suggesting that it should be interpreted with caution. Moreover, due to the methodological approach that we followed, two issues must be outlined regarding how solitariness was assessed in the present work.

First, during the Conspecific test, the social stimulus was not visible from the focal fish as it was placed in an opaque jar situated at the centre of the arena. This absence of visual contact between the focal fish and its conspecific allowed us to interpret the interaction as reflecting true social interest without any establishment of dominant-subordinate relationships. One could wonder whether the results would have been the same if the conspecific had been visible or was presented to the focal fish in a different manner (e.g. transparent partition or at a different location in the arena). It must be noted, however, that although not visible, the conspecific inside the jar could still interact with the focal fish through holes that allowed chemical cues and pressure waves to disseminate into the arena.

Secondly, one may ask if there could be a carry-over effect of the risk-responsiveness to the jar at day 2 on the response to the presence of a conspecific inside that jar at day 3. For example, fish with reduced interactions with the novel object at day 2 were considered as risk-averse. These individuals might have continued to show aversion to this object at day 3, despite the presence of a conspecific inside. Although, *Risk-taking* was evaluated on the first five minutes of the Novel object test (day 2), fish actually remained a total of 30 minutes in the arena, familiarizing with the object. It was therefore considered that at day 3, the jar was no more a novel object, allowing us to consider that interaction with the jar was then fully attributable to the presence of the conspecific inside.

With regard to our first hypothesis, control (C) fish interacted more with conspecifics than food-deprived (FD) fish. Juvenile European sea bass form shoals, a social behaviour which is believed to relies on fish voluntary decision to remain together (Réale et al., 2007). Grouping behaviour is increasingly considered as a flexible response by which individuals tune the trade-off between predator avoidance and resource acquisition (Krause et al., 2000b; Lima and Dill, 1990). Shoaling indeed contributes to maximising food acquisition through increased detection rate and, at the same time, enhances predator avoidance through greater vigilance in addition to dilution and confusion effects. However, grouping behaviour is also associated with stronger competition between conspecifics as well as with being more easily noticed by predators, shoals being more visually conspicuous than solitary individuals (Clifton and Robertson, 1993). The observation that food-deprived fish displayed reduced interactions with conspecific suggests that when food is scarce, individual may benefits from solitariness as it reduces competition and aggressiveness prompted by hunger (Webster and Hart, 2006).

Conflicting with our second hypothesis, experimental results revealed that food-deprivation had no impact on risk-taking and exploratory activity in sea bass. Individuals from the FD group were initially expected to be risk-prone and to display higher activity level than fish from the C group. It has indeed been hypothesized that higher level of activity and risk-taking favour habitat exploration and consequently enhance food encountering (Killen et al., 2011; McFarlane et al., 2004; van Dijk et al., 2002). Moreover, following starvation increased activity and risk-taking has been reported (Godin and Crossman, 1994; Killen et al., 2011; McFarlane et al., 2004). To explain this inconsistency between the present results and the literature, differences in experimental design must be considered. While in the present study activity and risk-taking were assessed from the viewpoint of novelty, using an unfamiliar environment or a novel object, the studies mentioned above measured spontaneous activity in a familiar environment and assessed risk-taking in response to attractive and/or repulsive stimuli. Due to these among-studies discrepancies in experimental designs, swimming activity and risk-taking were actually evaluated in different contexts in which fish may have expressed a different behavioural response. In the present study, the fact that exploratory activity and risk-taking did not change in starved sea bass suggests that after three weeks of food deprivation, the trade-off between fulfilling nutritional requirement and risk-taking in response to novelty was unchanged. It remains to be tested, however, whether this trade-off would have been resolved differently if fish energetic status had been aggravated further, by a longer starvation period for instance.

It has to be pointed out that *Exploratory activity* was nearly statistically different between C and FD fish (P=0.057). This suggests that compared to C fish, the exploratory tendency of starved individuals tended to be reduced (Fig. 1B and 1F). This result is in line with other studies where decreased activity after food-deprivation has been reported (Binner et al., 2008; van Dijk et al., 2002). Swimming is energetically costly and it would make sense that fish with reduced energy reserve lowered the expression of energetically demanding activities such as swimming. However, lowering exploratory activity also implies reduced chances of finding food. In the present study, no food was made available to the fish, possibly rendering increased swimming inappropriate. Yet, the strategy could have been different if food had been made available, augmenting the potential reward of increased exploratory activity.

Correlation among behaviours

The observed trade-off between *Risk-taking* and *Solitariness* in risk-prone individuals validated our third hypothesis. After three weeks of food restriction, we indeed demonstrated that risk-prone FD fish interacted less with conspecifics (increased solitariness) while risk-prone C fish interacted more with conspecifics. As already discussed above, food restriction does not affect risk-taking. This suggests, therefore, that the origin of the *Risk-taking-Solitariness* interaction in risk-prone fish lays in the modulating effect of fish nutritional status upon *Solitariness*.

Under control feeding condition, individuals that interacted the most with the novel object also exhibited the highest interest for conspecifics. This result is in accordance with observations reported by Cote and Clobert (2007) on *Lacerta vivipara*, but it contradicts studies were risk-prone fish were reported to ignore conspecifics and to engage in less interactions than risk-averse individuals (Budaev, 1997; Harcourt et al., 2009a; Wilson et al., 1993). Juvenile sea bass are gregarious fish that form shoals (Barnabé, 1980) and the sharing of the food is not always equal within a shoal (Bumann and Krause, 1993; Krause, 1993; Ward et al., 2004). It can be hypothesized that fish with high propensity to take risk also benefit from solitariness to find and secure food without competition. Similarly, Harcourt et al. (2009b) reported that hunger modulated shoaling behaviour differently in shy and bold three-spined sticklebacks. They showed that under normal feeding condition, shy and bold individuals both preferred to shoal with bold conspecifics. Under restrictive feeding condition, on the other hand, bold stickleback continued to prefer shoaling with bold fish while shy individuals displayed preference for shy conspecifics. These authors hypothesised that the change in shoaling preference observed in the starved shy individuals suggests that these fish perceived more acutely the potential intraspecific competition by the bold and responded by shoaling with shy and potentially less competitive conspecifics. This modulation of social behaviour by the interaction between feeding status and risk-taking behaviour is along the same line than our own results which indicate that in periods of food shortage, the potential reward associated with taking more risk and being less sociable may overcome the cost resulting from increased predation risk related with solitariness.

To conclude, present findings document how hunger may affect sociability in juvenile sea bass and they contribute to increase current knowledge regarding the interaction between feeding status and risk-taking and how it can drive social behaviour.

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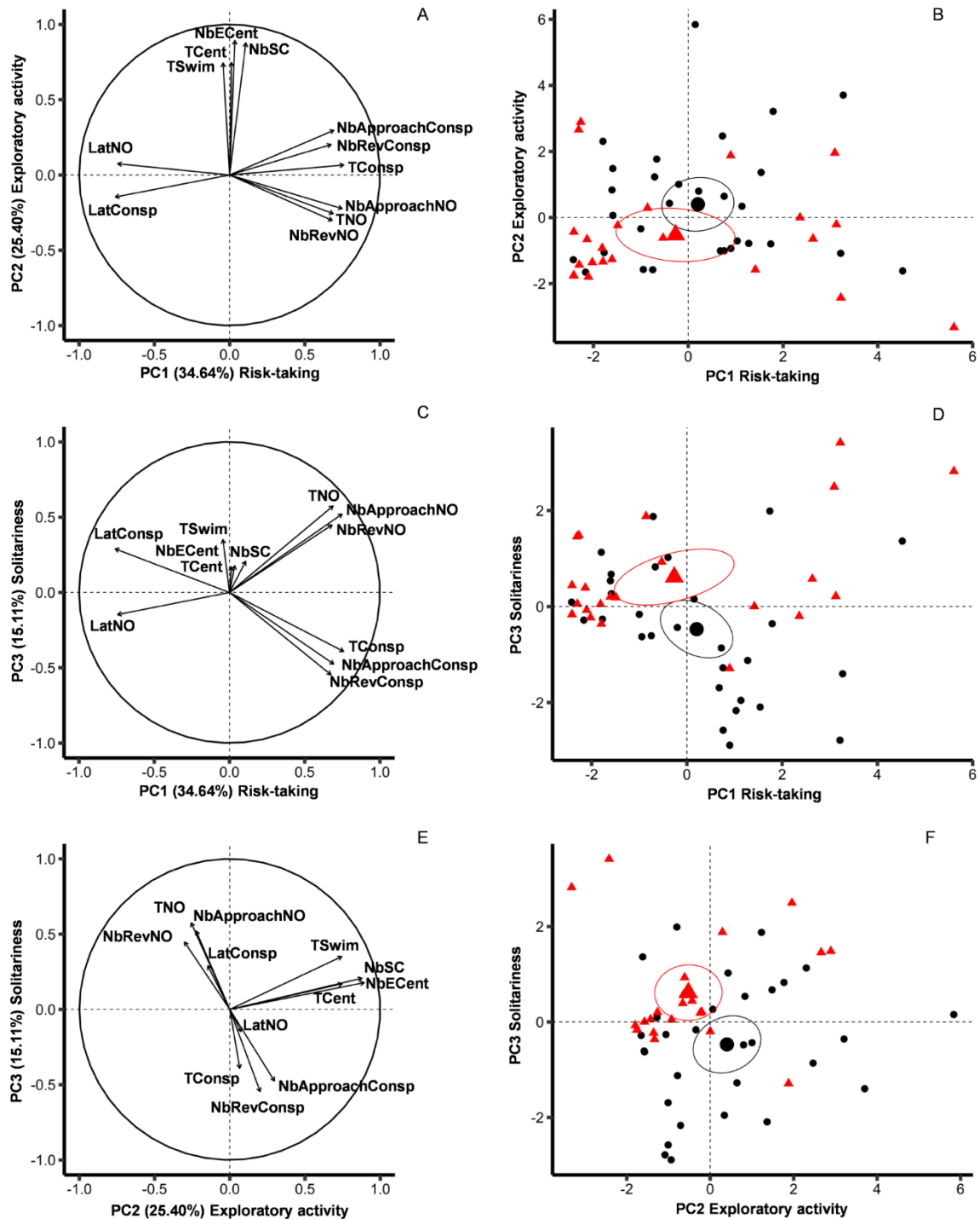
Figures

Fig. 1. Individuals' position along the *Risk-taking, Exploratory activity* and *Solitariness* axes. Left column (A, C, E): relationships between behavioural variables and their contribution to the PC. Right column (B, D, F): individuals' factor maps. Top line: *Exploratory activity vs Risk-taking*; middle line: *Solitariness vs Risk-taking*; bottom line: *Solitariness vs Exploratory activity*. Red triangles: food-deprived fish (*N*=23); black circles: fish from the control treatment (*N*=30). Confidence ellipses are plotted around group mean points.
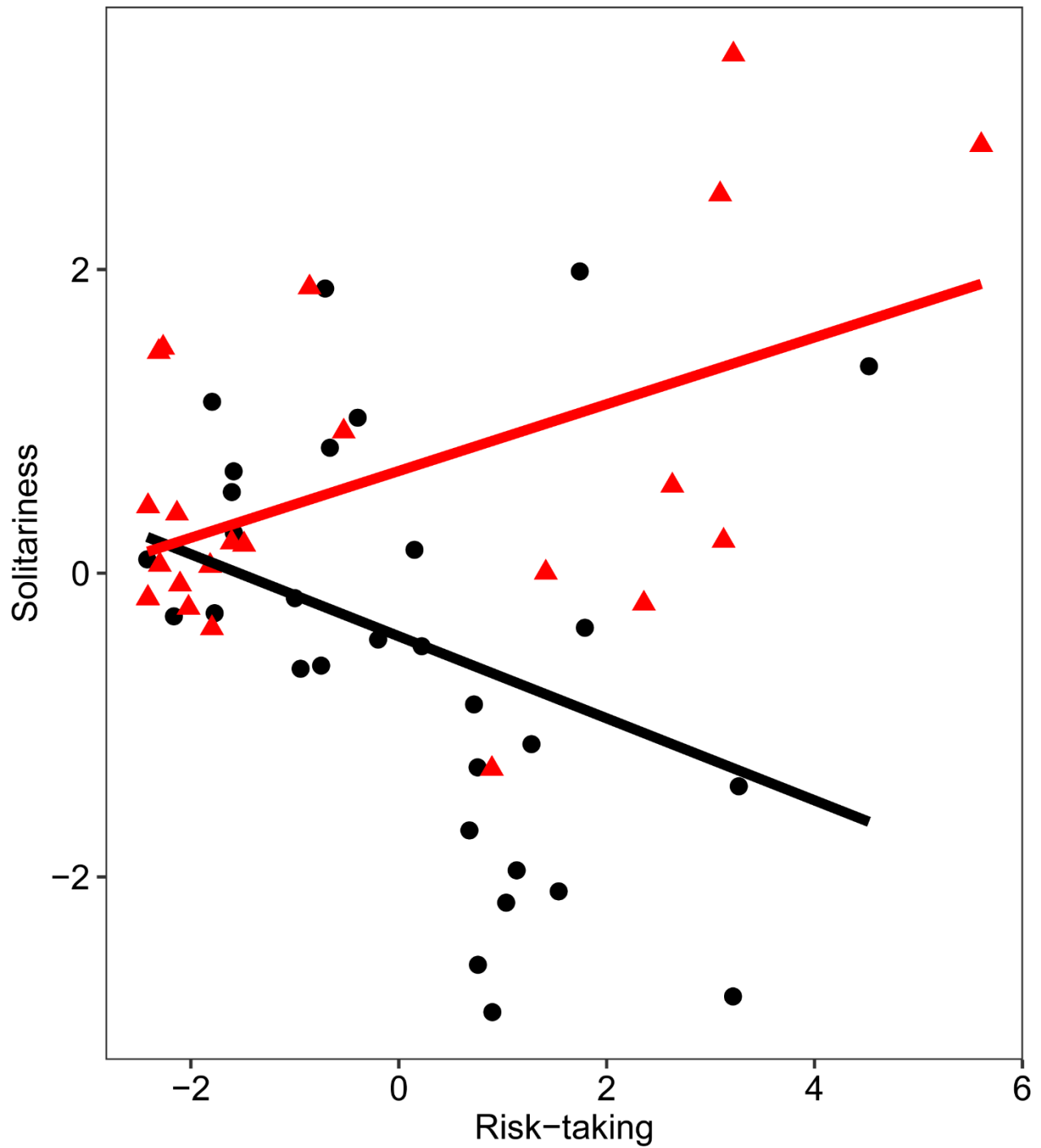
Fig. 2. Relationships between PC1 *Risk-taking* and PC3 *Solitariness* according to the feeding treatment. Black circles: scores of control fish (*N*=30); red triangles: scores of food-deprived fish (*N*=23); black line: control treatment; red line: food-deprived treatment.

Table 1. Eigenvalues of the axes of the principal components analysis

Principal component	Eigenvalue	Percentage of variance	Cumulative percentage of variance
1	4.157	34.639	34.639
2	3.049	25.404	60.043
3	1.814	15.114	75.157
4	0.912	7.604	82.761
5	0.625	5.211	87.972

The principal component analysis was performed with the twelve behavioural variables extracted from the Novel Environment (day 1), Novel Object (day 2) and Conspecific (day 3) trials.

Table 2. Coefficients of correlation of the three first principal components for each variable

Variables	PC1 *Risk-taking*	PC2 *Exploratory activity*	PC3 *Solitariness*
NbSC	0.108	**0.878**	0.207
TSwim	-0.044	**0.744**	0.351
TCent	0.012	**0.748**	0.171
NbECent	0.035	**0.894**	0.178
LatNO	**-0.744**	0.075	-0.147
NbApproachNO	**0.748**	-0.223	**0.521**
TNO	**0.689**	-0.257	**0.575**
NbRevNO	**0.682**	-0.302	**0.448**
LatConsp	**-0.761**	-0.146	0.290
NbApproachConsp	**0.693**	0.297	**-0.476**
TConsp	**0.759**	0.066	**-0.392**
NbRevConsp	**0.674**	0.202	**-0.546**

These three principal components (PC) represent 75.15% of the variance in the data. The variables used for the delineation of each component are in bold.

Table 3. Linear model describing the interaction between feeding regime, *Risk-taking* and *Solitariness*

Included variables	Excluded variables	Estimate	SE	t-value	P-value	
(Intercept)		-0.416	0.217	-1.915	0.061	.
Treatment		1.088	0.329	3.305	0.002	**
PC1 *Risk-taking*		-0.270	0.129	-2.097	0.041	*
Treatment * PC1 *Risk-taking*		0.490	0.164	2.981	0.004	**
	PC2 *Exploratory activity*	0.117	0.096	1.212	0.232	
	Treatment * PC2 *Exploratory activity*	-0.090	0.202	-0.446	0.657	

Estimates, SE (standard error), t-value and P-value were generated by the linear models fitting procedure. Included variables: significant contribution to the model; Excluded variables: non-significant contribution to the model.* indicates significant effect of the variables on PC3 (*Solitariness*; *P*<0.05).
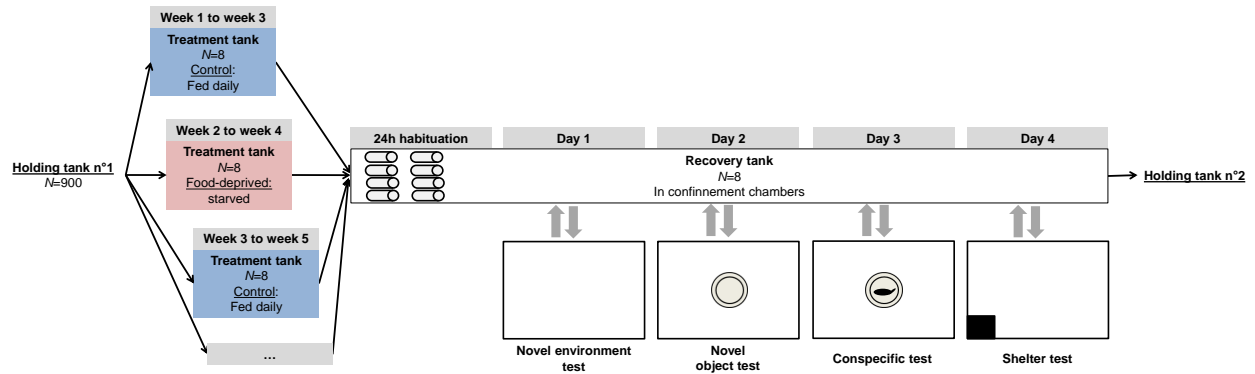
Fig. S1. Experimental protocol time line

On an alternative week basis, a set of 8 fish was taken from the holding tank n°1 and transferred to a treatment tank where it stayed 3 weeks. One treatment tank corresponding to the control group (C; fed daily; blue) or corresponded to the food-deprived group (FD; starved; red). Following this period of three weeks, individuals are transferred to 8 confinement chambers set side by side on the bottom of a recovery tank. After 24 hours of habituation, fish were successively submitted to four behavioural tests rand over four consecutive days. Day 1: novel environment test; Day 2: novel object test; Day 3: conspecific test; Day 4: shelter test. At the end of the testing period fish were returned to second holding tank.
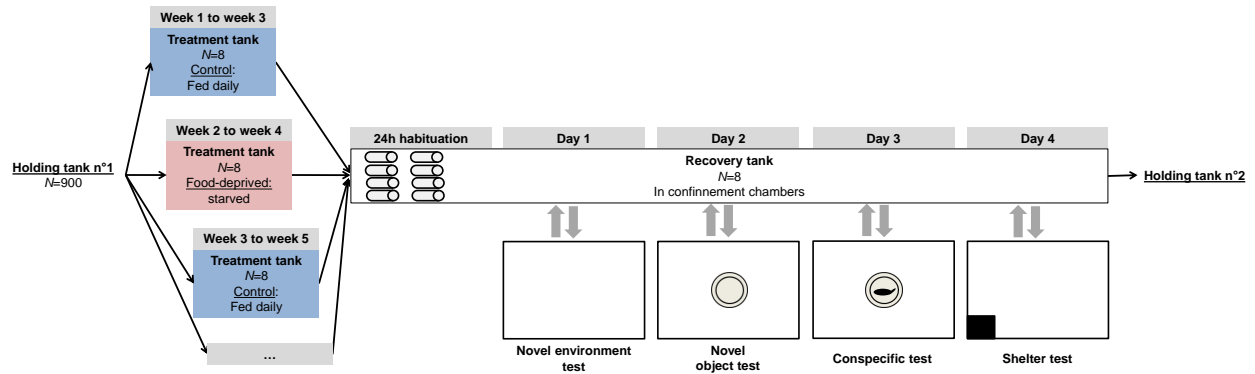
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