Behavioral Ecology and Sociobiology (2020) 74:67
https://doi.org/10.1007/s00265-020-02841-0

ORIGINAL ARTICLE

# Does consistent individual variability in pelagic fish larval behaviour affect recruitment in nursery habitats?

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Received: 29 May 2019 / Revised: 13 April 2020 / Accepted: 20 April 2020


## Abstract
Individual animals across all taxa differ consistently in behaviour, i.e. they show personality traits. This inter-individual variability has significant ecological and evolutionary consequences, since it affects a range of population-level processes. Here, we focus on the selection and recruitment of nursery habitats in temperate fish larvae. The "Sense Acuity and Behavioural Hypothesis" has proposed that fish larvae could detect and follow environmental cues to actively choose suitable nursery habitats. We empirically tested this hypothesis questioning if this non-random active process occurs and if it could be linked to consistency in individual behaviours. Individual larvae of the white seabream *Diplodus sargus* (Linnaeus, 1758) were tested repeatedly at different ages in a two-channel choice-chamber apparatus exposing them to a flow with different stimuli, as nursery habitats (lagoon, coastal), different temperatures or salinities and recording exploratory activity and preference in the different conditions. Most larvae changed behaviour during ontogeny, but they were also significantly consistent in their behaviour, revealing strong individuality; yet, no significant preference for the presented stimuli emerged, nor it was related to individuality. Exploratory activity was higher when larvae showed unresponsive or inconclusive behaviours, meaning that the larvae tried to find a different stimulus from the one that we were offering or had random habitat selection. Individual behavioural consistency could influence the process of searching for suitable nursery habitats and, consequently, dispersion and connectivity of white seabream population. Characterizing the behaviour of temperate pelagic marine fish larvae may shed light on fish recruitment variability, help refining larval dispersion models and possibly help understanding effects of climate change on population distribution and connectivity.

## Significance statement
A Chinese idiom says that "It is easier to change mountains and rivers than to alter one's character." What about fish? Well, fish can exhibit individuality traits that control autoecological and demecological processes. For example, shy fish have lower fitness while the rate of invasion progress is faster in populations with bolder individuals. Individuality studies rarely focused on fish larvae, except for coral fish. So, we tested if temperate fish larvae display consistent behaviour throughout ontogeny. This goal delves into the Sense Acuity And Behavioural Hypothesis which incorporated behaviour into the hypotheses deeming to explain fish recruitment variability. We found that temperate fish larvae display consistent individual behavioural differences in exploratory activity since early in ontogeny. This confirms the deterministic role of pelagic fish larvae behaviour on population connectivity processes, namely to control their dispersion and choose a nursery habitat.

**Keywords** Fish larvae · Personality · Recruitment · Environmental cues · Habitat choice

Communicated by J. Lindström

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s00265-020-02841-0) contains supplementary material, which is available to authorized users.

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Published online: 15 May 2020

## Introduction

Many fish species, such as coastal temperate fish species, have a bipartite life history (Radford et al. 2012): spawning occurs at the sea where the larvae hatch from planktonic eggs and spend time in the pelagic environment, subjected to current effects before they recruit in coastal ecosystems (Leis 2006; Teodósio et al. 2016). Recruitment in coastal nursery areas (i.e. coastal lagoons, estuaries, and rocky shore areas) enhances survival and growth thanks to the availability of food resources and protection from predators (Bradbury and Snelgrove 2001; Barbosa and Chícharo 2011; Chícharo et al. 2012; Teodósio et al. 2016).

The survival and growth during the larval and juvenile phases are crucial for spatial and temporal recruitment variability (Houde 2008; Teodósio et al. 2017), which affect the size and dynamics of local populations. Recruitment is defined as the addition of new individuals to the population, so its variability is influenced by the complex interaction of biological (e.g. starvation and predation) and physical processes related to larval transport and retention during early stages (Hale et al. 2008) and with the food web processes that sustain fish larvae (Santos et al. 2007). Thus, annual recruitment can be affected by small changes in growth and survival rates of fish larvae (Houde 2008). However, the movement between coastal spawning habitats and recruitment into coastal ecosystems is still poorly understood (James et al. 2008; Radford et al. 2012).

Several hypotheses have been proposed to explain the variability of coastal fish recruitment (see Morais 2020 for a detailed review)—i.e. critical period hypothesis (Hjort 1914), aberrant drift hypothesis (Hjort 1926), migration triangle hypothesis (Harden Jones 1968), match-mismatch hypothesis (Cushing and Dickson 1976; Cushing 1990), stable ocean hypothesis (Lasker 1978), stable retention hypothesis (Iles and Sinclair 1982), member/vagrant hypothesis (Sinclair and Iles, 1987), optimal environmental window hypothesis (Cury and Roy 1989) and ocean triads hypothesis (Bakun 1996). They all assume a passive and stochastic drift of larvae, without any active role of the individual larvae in the migration from spawning grounds to nursery ecosystems and the ability to find and swim toward them (Morais 2020). This paradigm has shifted with the sense acuity and behavioural (SAAB) hypothesis, which states that the recruitment of temperate fish larvae is unlikely if the larvae drift passively through water currents and that sense acuity of temperate fish larvae and their behavioural responses to nursery cues in coastal areas are essential for recruitment success (Teodósio et al. 2016). As the sensorial acuity and swimming capacity of larvae increase during ontogeny (Fisher et al. 2000; Gerlach et al. 2007; Teodósio et al. 2016; Baptista et al. 2019), it is expected that their behavioural ability to search for nursery habitats differs during development using a hierarchy of sensory cues to detect and navigate to these coastal nurseries (Teodósio et al. 2016).

Fish larvae use different senses to choose a suitable settlement habitat according to water characteristics/cues, such as olfaction (Atema et al. 2002; Gerlach et al. 2007; Dixson et al. 2008), vision (Whitfield 1994; Faillettaz et al. 2015), sound (Montgomery et al. 2006; Leis et al. 2011; Staaterman et al. 2014) and magnetism (Qin et al. 2015). Although all these senses contribute to habitat choice, olfaction has been recognised as the prevalent cue for locating nursery habitats (Atema et al. 2002; Lecchini et al. 2005b; Døving et al. 2006; Dixson et al. 2008). Fish larvae are capable of distinguishing and following several chemical stimuli (e.g. type of substrate, vegetation, conspecifics, predators, prey) present in water (Lecchini et al. 2005b; Døving et al. 2006; Gerlach et al. 2007; Radford et al. 2012). On the other hand, oceanographic factors such as current speed, turbidity, salinity, oxygen concentrations and temperature also influence habitat choice (Boehlert and Mundy 1988; Whitfield 1994; Gibson 1997; Atema et al. 2002; Bos and Thiel, 2006; Angeletti et al. 2017). Recent evidence showed that the detection and response to these cues may be changing due to global climatic changes (Munday et al. 2009; Pecl et al. 2017; Rossi et al., 2016; Gouraguine et al. 2019), affecting settlement behaviour and recruitment of fish larvae (O'Connor et al. 2015). For example, changes in water temperature and salinity have been reported to affect the behaviour and habitat choice patterns, in addition to critical physiological processes (Pecl et al. 2017).

Despite the increase of studies on larval settlement strategies over the past decades, most have been conducted on how coral-reef fish larvae detect and follow environmental cues for habitat selection (Atema et al. 2002; Dixson et al., 2008; Gerlach et al. 2007). However, only a few studies proposed that environmental cues could also play an important role in the recruitment of temperate fish larvae (James et al. 2008; Radford et al., 2012; Havel and Fuiman 2016; Morais et al. 2017) and that recruitment may be an active and behaviourally mediated process (Boehlert and Mundy 1988).

Individual animals across many taxa, including fish, differ consistently in behaviour, i.e. they show personality traits (Briffa and Weiss 2010; Carere and Maestripieri 2013). This inter-individual variability, which can be seen as a behavioural polymorphism, has significant ecological and evolutionary consequences, since it affects a range of population-level processes. More recently, empirical and theoretical work has suggested that personality traits can influence all phases of dispersal processes (departure, transience, settlement), and consequently spatial patterns of populations (Cote et al. 2010; Nanninga and Berumen 2014; Canestrelli et al. 2016). However, studies on fish personality traits have been mostly focused on juveniles (Biro et al. 2010; Wilson et al. 2011; Castanheira et al. 2013, 2016) or adults (Bell and Stamps 2004; Biro et al. 2004, 2006; Wilson et al. 2011), with few exceptions considering fish larvae (Sundström et al. 2004; Budaev and Andrew 2009; Pasquet et al. 2016). Sundström et al. (2004) found that in the brown trout *Salmo trutta* (Salmonidae) (Linnaeus, 1758), bold individuals were more likely to become dominant. Budaev and Andrew (2009) showed that the development of eggs and larvae of zebrafish *Danio rerio* (Cyprinidae) (Hamilton, 1822) in darkness increased shyness and reduced behavioural asymmetries (larvae respond in the same way to stimulus on the left and the right) in response to predators. Pasquet et al. (2016) showed that Northern pike *Esox Lucius* (Esocidae) (Linnaeus, 1758) larvae could be ranked along a gradient of boldness-shyness. The small size and the fragility of fish larvae with consequent technical difficulties for proper behavioural testing could explain the low number of studies to date (Pasquet et al. 2016). However, individual variation in larval behaviour may be essential to understand the dispersal and recruitment dynamics of fish populations (Nanninga and Berumen 2014; Pasquet et al. 2016) due to its influence on food acquisition, predator's avoidance (Biro et al. 2006; Stamps 2007), and consequently on habitat selection (Stamps 2006; Stamps and Groothuis 2010).

Under this general framework, we hypothesised that temperate fish larvae could detect and follow environmental cues to actively choose suitable nursery habitats and that their predisposition to follow environmental cues could be mediated by consistent individual differences in behaviours (e.g. exploration and activity – two typical personality traits, which are related to dispersal; Canestrelli et al. 2016). Thus, we aimed to (i) detect consistent individual differences in these behaviours in temperate pelagic fish larvae across ontogeny, (ii) test if and how these consistent individual differences relate to environmental changes (increase of water temperature or decrease of salinity) and (iii) test if they affect the ability to choose nursery habitats by detecting different environmental cues.

## Material and methods

### Model species

The white seabream *Diplodus sargus* (Linnaeus, 1758) is a demersal fish distributed in the Northeast Atlantic Ocean and Mediterranean Sea (Pajuelo and Lorenzo 2002). This species inhabits coastal rocky reefs, sandy bottoms and seagrass beds at depths down to about 150 m (Pajuelo and Lorenzo 2002) but is generally more abundant from the shore to 50 m depth in the Northeast Atlantic Ocean and Mediterranean Sea (Harmelin-Vivien et al. 1995). White seabream is abundant in the Portuguese coast, on the continental shelf (Leitão et al. 2007), lagoons and estuaries (Vinagre et al. 2010), and it sustains important recreational and commercial fisheries (Erzini et al. 1999; Veiga et al. 2010).

White seabream adults spawn in coastal areas from March to June (Morato et al. 2003, Faria et al. 2006), producing pelagic eggs that hatch after 3 days (Di Franco and Guidetti 2011), and larvae spend up to 4 weeks in the pelagic environment (González-Wangüemert et al. 2010). During the pelagic phase, eggs and larvae can disperse passively for 100–200 km through marine currents, before reaching favourable habitats for recruitment (Di Franco et al. 2012). During the post-flexion phase, when flexion of the notochord is completed and larva have good swimming abilities, they could swim to settlement places at shallow depths (0–2 m) on sandy-rocky bottoms (Harmelin-Vivien et al. 1995), coastal lagoons (Monteiro et al. 1990) and estuaries (Faria et al. 2006; Gonçalves et al. 2015). They remain in these habitats for about a year (Planes et al. 1999), after that they move towards deeper habitats to recruit into the adult population (Harmelin-Vivien et al. 1995). Thus, as most Sparidae, white seabream behaves as cyclic migrants, migrating to nursery habitats after metamorphosis, and spending the early stages of life in these environments (Pajuelo and Lorenzo 2004).

### Animals and housing conditions

White seabream larvae were obtained from natural spawns of wild broodstocks established at the Aquaculture Research Station (EPPO) of the Portuguese Institute for the Ocean and Atmosphere (IPMA) in Olhão (Portugal), comprising 12 individuals in a proportion of 1:2 (females/males) at a density of 1.5 kg $m^{-3}$. Larvae (21 DPH—days post-hatching) were collected at the EPPO, 24 h before the beginning of the experiment (Table 1) and kept on a 20-L tank at a quiet and temperature-controlled room where the experiments were conducted (CCMAR facilities, University of Algarve).

Forty larvae were randomly selected from the tank and individually housed in breeding containers (10 × 10 × 10 cm) in two tanks (each containing 110 L) with water from the Ria Formosa lagoon (Ramalhete Station, Portugal, 37°00′21.13″ N, 7°58′02.39″ W; R from now onwards; Table 2). During all experiments, the water temperature was kept similar in both tanks, at 19.4 (± 1.2) °C. Whenever possible, the same individual larvae were tested throughout all ages and conditions. Because of normal larval mortality during the experiment, the dead larvae were replaced by new larvae at ages 2 and 3 to maintain a sample size of 40, which led to a total 93 larvae used (Table 3). All larvae were tested on the same day for each of the four tests.

The larvae's mouth opens at three DPH (Ortiz-Delgado et al. 2003) when they start the exogenous feeding. Larvae were fed ad libitum with rotifers *Brachionus* sp. (Pallas, 1766) for the first 14 DPH, with rotifers, branchiops *Artemia* spp. (Leach, 1819) nauplii, and dry feed (Caviar from BernAqua) from 15 to 21 DPH, with *Artemia* spp. nauplii and dry feed until 37 DPH, and afterwards just with dry feed

**Table 1** Timeline (DPH—days post-hatching) of housing and choice-chamber test (test I-lagoon cue, test II-coastal cue, test III-increase of temperature, test IV-decrease of salinity) for white seabream *Diplodus sargus* (Linnaeus, 1758) larvae

| DPH | Day | Procedure | Age group |
|---|---|---|---|
| 21 | | Collected and housing | – |
| 22 | | Individual housing and acclimatization | Age 1 |
| 23 | 1 | Test I and test II | |
| 24 | 2 | Test I and test II | |
| 25 | 1 | Test III and test IV | |
| 26 | 2 | Test III and test IV | |
| 32 | | Individual housing and acclimatization | Age 2 |
| 33 | 1 | Test I and test II | |
| 34 | 2 | Test I and test II | |
| 35 | 1 | Test III and test IV | |
| 36 | 2 | Test III and test IV | |
| 42 | | Individual housing and acclimatization | Age 3 |
| 43 | 1 | Test I and test II | |
| 44 | 2 | Test I and test II | |
| 45 | 1 | Test III and test IV | |
| 46 | 2 | Test III and test IV | |
| 52 | | Individual housing and acclimatization | Age 4 |
| 53 | 1 | Test I and test II | |
| 54 | 2 | Test I and test II | |
| 55 | 1 | Test III and test IV | |
| 56 | 2 | Test III and test IV | |

with increasing granulometry as development progressed. This diet has proved to support the development and growth of white seabream larvae (Pousão-Ferreira et al., 2005).

## Design and experimental set-up

White seabream larvae underwent a series of tests at each of four ages (age 1– 22–26 DPH, age 2– 32–36 DPH, age 3– 42–46 DPH and age 4– 52–56 DPH; Table 1). At each age, a series of four tests were performed on four consecutive days after an acclimatization of one day, where the behaviour was also recorded. In each test, the subject was exposed to two different water conditions: typical nursery odour cues (test I and test II) or changes in physical water conditions (test III and test IV; Tables 1 and 2). In test I, larvae were subjected to control water (R) and water from the main channel of the Ria Formosa lagoon (L; Portugal, 37° 00′ 11.17″ N, 7° 59′ 09.17″ W) with the presence of dwarf eelgrass *Zostera noltii* (Hornemann, 1832). In test II, the larvae were subjected to the control water (R) and water from a coastal habitat (C) collected in tide pools of a rocky shore beach (Olhos de Água, Portugal, 37° 05′ 21.57″ N, 8° 11′ 27.56″W). In test III, we used the control water (R) at housing temperature and the same water with an increase of 4 °C (R + 4C), which represents the tendency for sea surface temperature rise during the last decades (1950–2010) during spring in the Portuguese coast (Baptista et al. 2018). In test IV, we used control water (R) at housing salinity (36) and the same water diluted to reach a salinity of 26 (R-10) that represents the proximity to estuarine conditions in the southern Portuguese coast (Morais 2007). The experimental water used in the tests was collected at each site in the day before tests, during the ebb tide, stored at ambient conditions before use to avoid temperature differences between water sources.

Each test series began with the individual housing of larvae and acclimatization to the chamber environment using control water (same water used in housing; Tables 1 and 2). At each given age, each test was repeated on the following day for testing short-term repeatability (Table 1).

The behavioural responses of white seabream larvae to different environmental conditions (odour cues and water physical properties) were evaluated using a two-channel choice-chamber apparatus (Fig. 1) based on the designed proposed by Gerlach et al. (2007). The choice-chamber was made with plexiglass [20 × 4 × 2.5 cm (L × W × H)] and had two frontal water inlets and a rear water outlet. The flow rate in each choice lane was 20 ml min$^{-1}$ for larvae at age 1 and 60 ml min$^{-1}$ for older larvae (ages 2, 3 and 4). With these flows, larvae swam freely between chamber areas. In each test, a single larva was gently taken from the breeding

**Table 2** Water conditions experienced in housing and choice-chamber testes (test I-lagoon cue, test II-coastal cue, test III-increase of temperature, test IV-decrease of salinity) for white seabream *Diplodus sargus* (Linnaeus, 1758) larvae

| Procedure | | Water conditions/stimuli | Code |
|---|---|---|---|
| Housing standard individual conditions | | Ria Formosa lagoon–Ramalhete | R |
| Test I | Control | Housing water | R |
| | Stimulus | Lagoon habitat–Ria Formosa main channel | L |
| Test II | Control | Housing water | R |
| | Stimulus | Coastal habitat–Olhos de Água rocky shore beach | C |
| Test III | Control | Housing water | R |
| | Stimulus | Housing water with an increase of 4 °C | R + 4C |
| Test IV | Control | Housing water | R |
| | Stimulus | Housing water with a decrease of 10 in salinity | R-10 |

**Table 3** Number of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae tested across ontogeny (age 1- 22-26 DPH—days post-hatching, age 2- 32-36 DPH, age 3- 42-46 DPH, and age 4- 52-56 DPH) in each binary test (test I-lagoon cue, test II-coastal cue, test III-increase of temperature, test IV-decrease of salinity). The number of replaced larvae is in brackets

| Stimulus | Age 1 | | | Age 2 | | | Age 3 | | | Age 4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Day 0 | Day 1 | Day 2 | Day 0 | Day 1 | Day 2 | Day 0 | Day 1 | Day 2 | Day 0 | Day 1 | Day 2 |
| Acclimatization | 40 | – | – | 40 (27) | – | – | 40 (26) | – | – | 29 | – | – |
| Test I | – | 38 | 35 | – | 40 | 34 | – | 38 | 34 | – | 28 | 26 |
| Test II | – | 38 | 36 | – | 40 | 37 | – | 37 | 35 | – | 29 | 27 |
| Test III | – | 26 | 24 | – | 28 | 25 | – | 32 | 31 | – | 25 | 25 |
| Test IV | – | 24 | 24 | – | 30 | 23 | – | 31 | 31 | – | 25 | 25 |

container with a transparent plastic spoon, placed in the centre of the choice-chamber and left undisturbed for 300 s to habituate to the flow and to the water sources (odour or physical cues, pre-test). At the end of this pre-test phase, the behaviour of larvae was observed for 120 s (trial 1). During the next 120 s, the water source positions were switched to control for possible side preferences not associated with odour cues. After that, the procedure was repeated: 300 s for pre-test, followed by 120 s for behavioural observation (trial 2).

All phases were recorded with a GoPro HERO4 Silver Edition Adventure camera and later analysed with the software BORIS v4.1.1 (Behavioral Observation Research Interactive Software; Friard and Gamba 2016) by one single observer (VB). To minimise observer bias, blinded methods were used when all behavioural data were recorded and analysed.

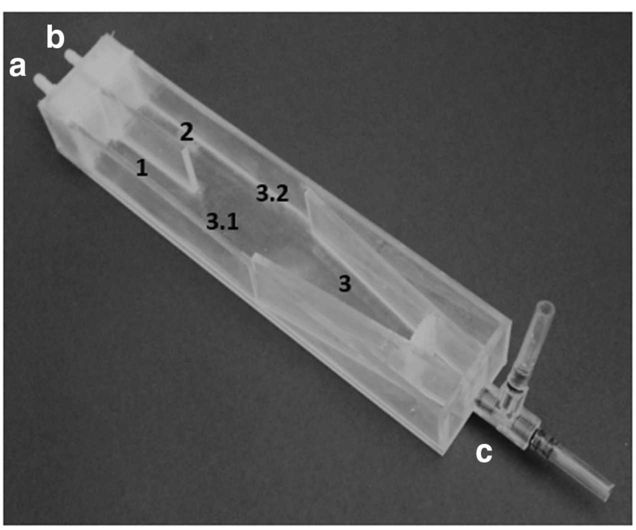


**Fig. 1** Choice-chamber used in preference tests of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae to different odour cues (based on the design by Gerlach et al. 2007). The dimensions of the chamber are 20 × 4 × 2.5 cm (L × W × H). Legend: **a**, **b** water intake, **c** water outlet, areas (**1**) and (**2**) are choice lanes, areas (**3**), (**3.1**) and (**3.2**) are considered unresponsive areas [area (**3.1**) is more influenced by source (**a**), while area (**3.2**) is more influenced by source (**b**)]

## Data collection–behavioural observations

We recorded the position of larvae in the choice-chamber (stimulus 1, stimulus 2 or unresponsive areas; Fig. 1) throughout the observation period (120 s) in each trial.

We used the Preference Index (PI) developed by Morais et al. (2017) to estimate the preference of white seabream larvae to different odour cues. Importantly, this index considers the unresponsive (time spent in unresponsive areas) and inconclusive behaviours (when the larvae spent equal time in each choice area), overlooked in most habitat choice studies (e.g. Atema et al. 2002; Gerlach et al. 2007; James et al. 2008; Radford et al. 2012). The Preference Index (PI) was calculated using Eq. 1,

$$\boldsymbol{PI} = \left[\left(\sum t_{CW} - \sum t_{SW}\right) \times T^{-1}\right] \times \left(1 - \sum t_{UNR} \times T^{-1}\right) \quad (1)$$

where $T$ is the sum of both trials' duration (240 s), $\sum t_{CW}$ is the total time that larva spent in control area, $\sum t_{SW}$ is the total time that larva spent in the stimulus area and $\sum t_{UNR}$ is the total time that larvae spent in the unresponsive area in both trials. PI varies between − 1 (preference for control water during the entire trial) and + 1 (preference for stimulus water during the entire trial), while 0 indicates that larvae showed unresponsive behaviour or no preference for an odour cue.

We measured exploration as the total number of areas of the choice-chamber visited by a larva (maximum of five areas; Fig. 1) and activity as the number of crossings between areas of the chamber. We combined these two measurements in an Exploratory Activity Index (EAI) expressed by Eq. 2:

$$\boldsymbol{EAI} = \frac{NA}{NAmax} \times \frac{NC}{NCmax} \quad (2)$$

where NA is the number of areas of the chamber visited by a larva (exploration), $NA_{max}$ the number of areas available in the chamber (five areas: 1, 2, 3.1, 3.2 and 3; Fig. 1), NC is the number crossings (activity) and $NC_{max}$ the number of movements done by the larva who changed the most between chamber areas during the entire test. EAI varies between 0 (low exploratory activity) and 1 (high exploratory activity).

## Data analysis

Chi-square tests (data not shown) were performed to detect the differences in the response of each larva to odour cues between trials. Larvae with the same response in both trials were analysed adding the observations from each trial (240 s in total). On the other hand, the larvae that showed different responses in each trial were considered inconclusive in the response to a specific odour cue and excluded from the analyses of that cue (Morais et al. 2017; Online Resource Table A1).

Since the assumptions of ANOVA were not satisfied for our dataset, we used the Kruskal-Wallis rank sum test to look for differences in behavioural responses of white seabream larvae between each test including their repetition on the following day (results not shown). No differences were observed between each test and its repetition ($p > 0.05$), so we averaged the two test days for the following analysis.

The differences in absolute frequencies between ages (age 1, age 2, age 3, age 4) in different stimuli (test I, test II, test III, test IV) and between stimuli in different ages were also analysed with Chi-square tests. Bonferroni corrections (Snedecor and Cochran 1989) were applied to the significance level ($p < 0.05$) to minimise the chance of obtaining a significant correlation due to random processes.

Linear mixed-effects models with multiple response variables (multivariate mixed models) were performed to evaluate the relationship among activity (ACT), exploration (EXP) and exploratory activity index (EAI) at individual level, as follows: value ~ trait − 1 + (trait-1|units), where value represents the numerical variable of the five measures of each unit (individual), trait is the categorical variable containing ACT, EXP and EAI inserted as fixed effect, while units is a random effect where each individual is inserted as a categorical variable. EAI ranged from 0 to 1, and for this reason, ACT and EXP were standardised to an equal range (0–1 scale) according to $x' = x - \min(x) / [\max(x) - \min(x)]$ where $x$ is the original value and $x'$ is the standardised value (Williams 2011). Since there were positive correlations between indices (Online Resource Table A3), we only used the EAI data in subsequent analysis.

Repeatability was calculated with generalised linear mixed-effects models. PI or EAI was inserted as response variable, age as fixed effect and individuals as random effect. Confidence intervals and intercepts of each model were obtained after 1000 bootstrap replicates (Stoffel et al. 2017). Mixed-effects models were also performed to test whether PI and EAI are related to nursery habitat (lagoon and coastal habitats—tests I and II, respectively) and environmental changes (increase of temperature and decrease of salinity—tests III and IV, respectively) across ontogeny (ages). Significance of the models was evaluated by the Satterthwaite's method (Kuznetsova et al. 2017). Random variance within and among individuals was also estimated by the model. Statistical significance was set at $\alpha = 0.05$.

All analyses were carried out under the R environment for statistical computing, using the packages 'lme4' to perform the mixed-effects models and 'rptR' for repeatability estimation (Bates et al. 2015; R Core Team 2019).

## Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author on request.

## Results

The behaviour of white seabream larvae was predominantly unresponsive (above 50.4%) or inconclusive (above 18.5%) in all ages and tests (Fig. 2). Overall, unresponsive behaviour decreased across ontogeny for tested habitats (test I—lagoon cue: from 67.8% at age 2 to 54.3% at age 4; and test II—coastal cue: from 58.5% at age 2 to 50.4% at age 4) (Fig. 2a, b) and increased for tested environmental conditions (test III—increase of temperature: from 56.3% at age 1 to 60.3% at age 3; and test IV—decrease of salinity: from 56.3% at age 2 to 60.3% at age 4) (Fig. 2c, d). Generally, the inconclusive behaviour decreased until age 3 (from 34.5 ± 6.1 to 21.0 ± 2.2%; mean ± standard deviation) and then increased at age 4 in all tests (test I—lagoon cue: 33.1%; test II—coastal cue: 31.9%; test III—increase of temperature: 35.2%; and test IV—decrease of salinity: 30.0%) (Fig. 2). This behaviour accounts for those larvae without a clear preference for any chamber areas. Larvae tended to prefer lagoon water (test I) during age 1 (6.8% compared to 2.6% for control water) and control water during other tested ages (6.9–12.8%; Fig. 2a). For coastal water (test II), increase of temperature (test III) and decrease of salinity (test IV) tests, larvae showed preference for control water (6.7–12.5%) over coastal water (test II; Fig. 2b), lower water temperature (test III; 0–14.3%; Fig. 2c) and higher water salinity (test IV—2.0–9.3%; Fig. 2d). The behaviour of white seabream larvae differed significantly between age 3 and age 4 for test IV (decrease of salinity: $\chi^2$ test, $p < 0.0001$) and between test II and test IV for age 4 ($\chi^2$ test, $p = 0.012$; Table 4).

The Preference Index (PI) ranged between − 1.00 and 1.00 (Fig. 3). Contrary to what observed in most of the tests across ages (Fig. 3), white seabream larvae preferred water with external cues over control water at age 1 in test I (lagoon cue: − 0.02 ± 0.23; Fig. 3a). The linear mixed-effect models showed tendential differences for the PI at age 2 in the lagoon cue test (test I: $p = 0.077$; Table 5), where 6.9% of the larvae at age 2 preferred control water and none of the larvae preferred lagoon water (PI: 0.06 ± 0.18; Figs. 2a and 3a). The linear mixed-effect models also showed significant differences for the PI at age 3 in the

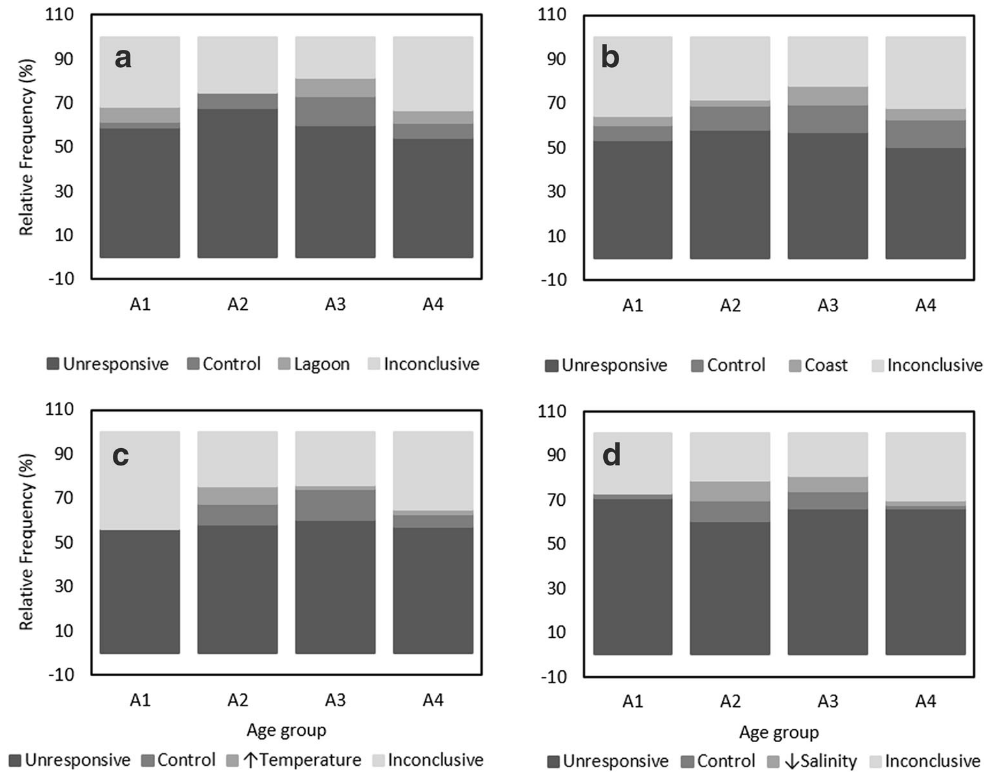


**Fig. 2** Preference of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae for different habitat conditions (**a** test I, lagoon cue; **b** test II, coastal cue; **c** test III, increase of temperature; and **d** test IV, decrease of salinity) in choice-chamber experiments along ontogeny (age 1– 22–26 DPH—days post-hatching, age 2– 32–36 DPH, age 3– 42–46 DPH and age 4 –52–56 DPH)

increased water temperature test (test III: $p = 0.033$; Table 5). At age 3, larvae showed higher preference for control water (lower temperatures; test III: $0.10 \pm 0.26$; Fig. 3c).

In general, the exploratory activity index (EAI) increased along ontogeny (from age 1 to age 4) independently of the tested conditions (Fig. 4). In the four tests, larvae with unresponsive or inconclusive behaviours showed higher values of EAI than larvae with a preference for control or stimulus water, except for age 1 in test IV (decrease of salinity), where the larvae with a preference for control water showed higher EAI (Fig. 4). The linear mixed-effect models showed significant differences for EAI in all tested stimuli, especially at age 4 ($p < 0.0001$ for test I—lagoon cue, test II—coastal cue, and Test III—increase of temperature; and $p = 0.004$ for test IV—decrease of salinity). Significant differences were also found at age 1 ($p = 0.016$ for test I and test II; $p = 0.033$ for test III; Table 6) and age 3 ($p = 0.004$ for test IV; Table 6).

Significant short-term repeatability of EAI occurred at all ages ($p < 0.0001$), increasing along ontogeny from 0.30 at age 2 to 0.72 at age 4 (Table 7; Online Resource Fig. A1). The mixed-effect models including the individual as random effects explained 35% of the variance in test I-lagoon cue (i.e. repeatability was 0.35; $p < 0.0001$), 37% of the variance in test II-coastal cue (i.e. repeatability was 0.37; $p < 0.0001$), 62% of the variance in test III-increase of temperature (i.e. repeatability was 0.62; $p < 0.0001$), and 24% of the variance in test IV-decrease of salinity (i.e. repeatability was 0.25; $p = 0.028$) (Table 6; Online Resource Fig. A2).

## Discussion

Contrary to our main hypotheses, white seabream larvae did not show any preference for either lagoon or rocky shore habitats, neither towards increased water temperature or decreased water salinity. However, the main finding of this study was that during early phases of ontogeny, white seabream larvae exhibited a highly consistent inter-individual variability in behaviours across age and tests, suggesting a strong individuality. This previously unsuspected individual consistency highlights the need to consider for the possible consequences of this individuality, especially when inferring about larval dispersal processes and selection of settlement areas to recruit.

### Response to habitat and environmental cues

In general, white seabream larvae did not show a clear preference for any stimuli, contrary to the expectation that they would prefer lagoon and coastal habitats, which are used as nursery habitats across southern Europe (Monteiro et al. 1990; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al. 1995; Faria et al. 2006; Gonçalves et al. 2015). Despite this overall lack of preference, we observed tendential differences for the Preference Index (PI) at age 2 in test I (lagoon cue). At this age, white seabream larvae preferred control water (6.9%) instead of Ria Formosa lagoon water collected in an area with seagrass beds (0%). Although we expected a preference for lagoon water with a seagrass cue, like silver seabream *Pagrus*

**Table 4** Chi-square test results on the absolute frequency of behaviours exhibited by white seabream *Diplodus sargus* (Linnaeus, 1758) larvae (unresponsive, preference for control water, preference for stimulus water and inconclusive behaviour) in choice-chamber experiment trials for each test (test I-lagoon cue, test II-coastal cue, test III-increase of temperature, test IV-decrease of salinity) and along ontogeny (age 1–22–26 DPH—days post-hatching, age 2– 32–36 DPH, age 3– 42–46 DPH and age 4– 52–56 DPH). *p* values were corrected using the Bonferroni corrections. Significant differences are highlighted in italics

| Comparisons | *p* | Comparisons | *p* |
|---|---|---|---|
| Test I | | Age 1 | |
| Age 1 vs. age 2 | 0.799 | Test I vs. test II | 0.926 |
| Age 1 vs. age 3 | 0.149 | Test I vs. test III | 0.257 |
| Age 1 vs. age 4 | 0.125 | Test I vs. test IV | 0.110 |
| Age 2 vs. age 3 | 0.386 | Test II vs. test III | 0.402 |
| Age 2 vs. age 4 | 0.042 | Test II vs. test IV | 0.026 |
| Age 3 vs. age 4 | 0.160 | Test III vs. test IV | 0.302 |
| Test II | | Age 2 | |
| Age 1 vs. age 2 | 0.636 | Test I vs. test II | 0.790 |
| Age 1 vs. Age 3 | 0.259 | Test I vs. test III | 0.066 |
| Age 1 vs. age 4 | 0.201 | Test I vs. test IV | 0.049 |
| Age 2 vs. age 3 | 0.635 | Test II vs. test III | 0.066 |
| Age 2 vs. age 4 | 0.111 | Test II vs. test IV | 0.040 |
| Age 3 vs. age 4 | 0.332 | Test III vs. test IV | 0.986 |
| Test III | | Age 3 | |
| Age 1 vs. age 2 | 0.353 | Test I vs. test II | 0.961 |
| Age 1 vs. age 3 | 0.400 | Test I vs. test III | 0.227 |
| Age 1 vs. age 4 | 0.927 | Test I vs. test IV | 0.896 |
| Age 2 vs. age 3 | 0.446 | Test II vs. test III | 0.246 |
| Age 2 vs. age 4 | 0.488 | Test II vs. test IV | 0.749 |
| Age 3 vs. age 4 | 0.054 | Test III vs. test IV | 0.793 |
| Test IV | | Age 4 | |
| Age 1 vs. age 2 | 0.780 | Test I vs. test II | 0.840 |
| Age 1 vs. age 3 | 0.279 | Test I vs. test III | 0.220 |
| Age 1 vs. age 4 | 0.985 | Test I vs. test IV | 0.020 |
| Age 2 vs. age 3 | 0.458 | Test II vs. test III | 0.083 |
| Age 2 vs. age 4 | 0.182 | Test II vs. test IV | *0.012* |
| Age 3 vs. age 4 | *0.000* | Test III vs. test IV | 0.851 |

*auratus* (Sparidae) (Forster, 1801) (Radford et al. 2012), some studies found that most post-flexion gilthead seabream *Sparus aurata* (Sparidae) (Linnaeus, 1758) larvae preferred rocky coastal water over Ria Formosa lagoon water with seagrass cues (Morais et al. 2017) or had a weak reaction to seagrass cues in the Mediterranean Sea (Díaz-Gil et al. 2017). Yet, some species seem to ignore odour cues in detriment of another sensory stimulus. For example, linesnout goby *Elacatinus lori* (Gobiidae) (Colin, 2002) post-flexion larvae, a coral reef species, select sponge habitats using visual rather that odour cues (Majoris et al. 2018), similarly to other coral reef species (Lecchini et al. 2005a, 2014; Igulu et al. 2011).

Regarding environmental and climatic changes, salinity and temperature variability are known to influence the recruitment of fish larvae into nurseries areas (Maynou et al. 2014; Baptista et al. 2016; Leitão et al. 2016; Pecl et al. 2017) due to their effects on behaviour, physiology, distribution and migration (Bertram et al. 2001; Hunt von Herbing 2002; Pecl et al. 2017). Lower salinity plumes signal the presence of rivers along with coastal areas (Sabates 1990), while changes of salinity along the water column might indicate the direction of currents and water sources that could be used as environmental cues (Hughes 1969). However, our results did not indicate any clear preference for salinity changes (decrease of salinity or control water). This could mean that white seabream larvae reach estuaries through other cues. On the other hand, white seabream larvae preferred lower water temperature (i.e. control temperature), which might cause negative impacts in a situation of warming coastal waters (Leitão et al. 2016). Indeed, the increase of sea surface temperature over recent decades, approximately 0.4 °C by decade, coincided with a decrease of white seabream landings in the following years (Leitão et al. 2016; Baptista et al. 2018).

The remarkable predominance of unresponsive (no preference for stimulus or control areas) and inconclusive behaviours (without a clear preference for any chamber areas) have been reported by Morais et al. (2017) and overlooked by Atema et al. (2002), Gerlach et al. (2007) and Radford et al. (2012). The prevalence of these behaviours showed by most post-flexion larvae could mean that their olfactory stimulus must be complemented with ecosystem soundscapes (e.g. living animals—Simpson et al. 2005; Lillis et al. 2014; Atema et al. 2015; waves breaking on the coast—Montgomery et al. 2006), visual cues (e.g. water turbidity, bottom features, detection of conspecifics) (Whitfield 1994; Atema et al. 2015), magnetism (Crisp 1974; Qin et al. 2015), pressure gradients (Burke et al. 1995) or oceanic currents (Crisp 1974). We also observed that the exploratory activity was higher when larvae showed unresponsive or inconclusive behaviours. This might indicate that larvae were trying to find different stimulus (as described above) or were showing a random habitat selection. Indeed, unresponsive individuals have been linked to change their behaviours due to a random process (Wolf et al. 2008).

As expected, the exploratory activity increased across ontogeny and reached a maximum at age 4 (52–56 DPH), since the swimming capabilities (speed and endurance) of white seabream larvae also increase across ontogeny (Baptista et al. 2019). Increased exploratory activity is likely connected with the timing when different sensorial organs develop during ontogeny. These observations support the SAAB hypothesis, which proposed that the ability to detect cues increases with ontogeny, and the response to cues increases with increasing swimming capabilities (Teodósio et al. 2016). Although the exploratory activity increased with age across all tests, only the test with different temperatures (test III)

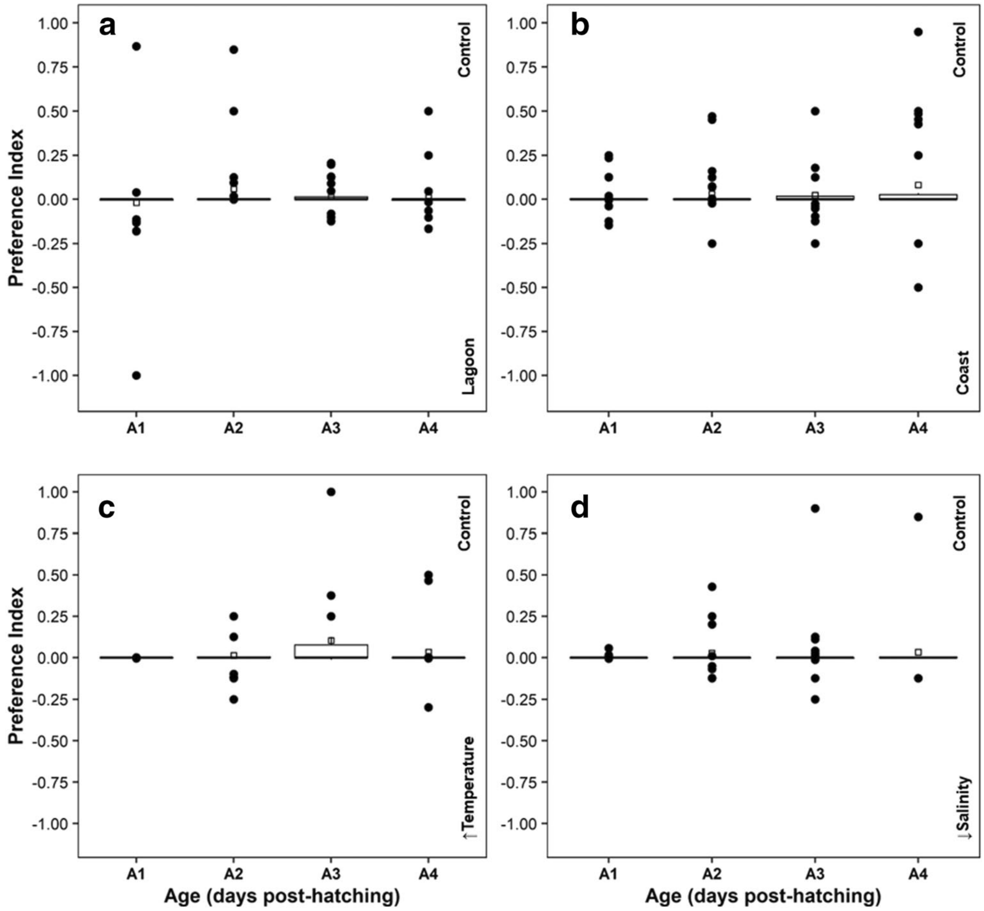


**Fig. 3** Preference Index of white seabream *Diplodus sargus* (Linnaeus, 1758) larvae in choice-chamber experiment trials for each test (**a** test I, lagoon cue; **b** test II, coastal cue; **c** test III, increase of temperature; and **d** test IV, decrease of salinity) and across ontogeny (age 1– 22–26 DPH—days post-hatching, age 2– 32–36 DPH, age 3– 42-46 DPH and age 4– 52–56 DPH). Negative values of this index indicate a preference for stimulus water, while positive values indicate a preference for control water. The mean is represented by open squares, the median is represented by the thick black line, the boxes represent the 1st and 3rd quartiles, and full black circles represent the outliers (values > 1.5 times and < 3 times the interquartile range beyond either end of the box)

induced significant differences at age 1, age 3 and age 4. Warmer water has been related to increase the activity of some fish species (Biro et al. 2007, 2010; Pasquet et al. 2016), either due to feeding behaviours (Theodorou et al. 2012; Reynisson and Ólafsdóttir 2018) or typical effects upon the metabolism of ectothermic animals (O'Connor et al., 2007; Biro and Stamps 2010). Thus, in a context of current environmental and climatic changes, the increase of water temperature in coastal areas may alter the responses of white seabream larvae, and also of other species, to nursery habitat cues.

In future studies, we should strive to add more complex experimental designs when testing chemical, visual and sound cues along ontogeny (e.g. offshore water cues; presence/absence of conspecifics, prey and predators), either for wild or laboratory-reared larvae (Díaz-Gil et al. 2017; Morais et al. 2017). Finally, consistent individual differences in behaviours related to dispersal, such as activity and exploration, must be taken into account in such experiments simultaneously to more traditional metrics (i.e. time spent following each cue; Morais et al. 2017).

## Individual behavioural consistency

White seabream larvae showed consistent behaviours when subject to different environmental stimuli through time, indicating the emergence of personality traits early in their development. This finding confirms the few existing studies that showed consistent individual behavioural differences in brown trout (Sundström et al. 2004), zebrafish (Budaev and Andrew 2009) and Northern pike larvae (Pasquet et al. 2016). Gilthead seabream also showed consistent individual behavioural differences at least during the juvenile phase (Castanheira et al. 2016).

**Table 5** Results of the linear mixed-effect models applied to evaluate the effects of the stimulus (test I-lagoon cue, test II-coastal cue, test III-increase of temperature, and test IV-decrease of salinity) on white seabream *Diplodus sargus* (Linnaeus, 1758) larval behaviour along ontogeny (age 1– 22–26 DPH—days post-hatching, age 2– 32–36 DPH, age 3– 42–46 DPH, and age 4– 52–56 DPH) using Preference Index (PI) as response variable. β: estimated beta effects, $\sigma^2$: estimated variance, SE: standard error, df: degrees of freedom, *p*: significance. Significant results and tendencies are highlighted in italics

| Stimulus | Model components | Estimate | SE | df | *t* | *p* |
|---|---|---|---|---|---|---|
| Lagoon cue | *Fixed effects* | *β* | | | | |
| | Intercept | − 0.017 | 0.028 | 122.0 | − 0.60 | 0.549 |
| | Age 2 | 0.072 | 0.040 | 42.6 | 1.81 | *0.077* |
| | Age 3 | 0.029 | 0.041 | 119.9 | 0.71 | 0.477 |
| | Age 4 | 0.035 | 0.045 | 111.3 | 0.77 | 0.444 |
| | *Random effects* | $\sigma^2$ | | | | |
| | Intercept (among-individual) | 2.836e-06 | | | | |
| | Residual (within-individual) | 0.028 | | | | |
| Coastal cue | *Fixed effects* | *β* | | | | |
| | Intercept | 0.021 | 0.028 | 123.8 | 0.73 | 0.463 |
| | Age 2 | 0.012 | 0.037 | 113.7 | 0.32 | 0.748 |
| | Age 3 | − 0.004 | 0.039 | 123.9 | − 0.11 | 0.910 |
| | Age 4 | 0.056 | 0.042 | 123.6 | 1.33 | 0.184 |
| | *Random effects* | $\sigma^2$ | | | | |
| | Intercept (among-individual) | 0.004 | | | | |
| | Residual (within-individual) | 0.022 | | | | |
| Increase of temperature | *Fixed effects* | *β* | | | | |
| | Intercept | − 0.002 | 0.038 | 88.9 | − 0.05 | 0.956 |
| | Age 2 | 0.011 | 0.052 | 71.8 | 0.22 | 0.823 |
| | Age 3 | 0.110 | 0.051 | 88.3 | 2.16 | *0.033* |
| | Age 4 | 0.039 | 0.055 | 88.3 | 0.71 | 0.483 |
| | *Random effects* | $\sigma^2$ | | | | |
| | Intercept (among-individual) | 0.003 | | | | |
| | Residual (within-individual) | 0.028 | | | | |
| Decrease of salinity | *Fixed effects* | *β* | | | | |
| | Intercept | 0.004 | 0.030 | 97.9 | 0.16 | 0.869 |
| | Age 2 | 0.023 | 0.040 | 88.6 | 0.59 | 0.557 |
| | Age 3 | 0.012 | 0.040 | 97.4 | 0.31 | 0.760 |
| | Age 4 | 0.025 | 0.042 | 97.7 | 0.59 | 0.554 |
| | *Random effects* | $\sigma^2$ | | | | |
| | Intercept (among-individual) | 4.09e-04 | | | | |
| | Residual (within-individual) | 0.019 | | | | |

We found relatively high coefficients of repeatability (average: 0.42 ± 0.17), similar to the average value of 0.37 reported in the meta-analysis of Bell et al. (2009), which includes both vertebrates and invertebrates. Short-term repeatability of exploratory activity increased with ontogeny with a maximum at age 4 (0.72), coinciding with the maximum levels of exploratory activity. This suggests that larval behaviour depends on the physical capabilities of individuals (Pasquet et al. 2016), as the exploratory activity index was calculated taking into account the number of zones visited and the number of changes between areas. As explained, the physical capabilities of fish larvae and their perception of the surrounding environment increase with increasing larval development. These changes could be linked to their physiological needs (e.g. food, shelter) that changes along ontogeny.

Bell et al. (2009) showed that the repeatability is significantly greater than 0 for a large range of taxa and behaviours. We showed that the repeatability coefficients varied among the tested stimuli, being higher for the increase of temperature (0.62) and lower for the decrease of salinity (0.24). In fact, it has been described that personality varies depending to environmental conditions (Pasquet et al. 2016), as individuals may differ in their sensitivity to environmental stimuli and consequently respond differently to changes in stimuli (Mathot et al. 2012). Biro et al. (2010) showed that activity, boldness and aggressiveness of damselfishes (*Pomacentrus moluccensis* and *Pomacentrus bankanensis*) were modified by an increase in water temperature of approximately 3 °C or less. These behavioural differences do not mean that individuals showed different personality depending on the stimuli, but they can show specific responses to different stimuli (Pasquet et al.

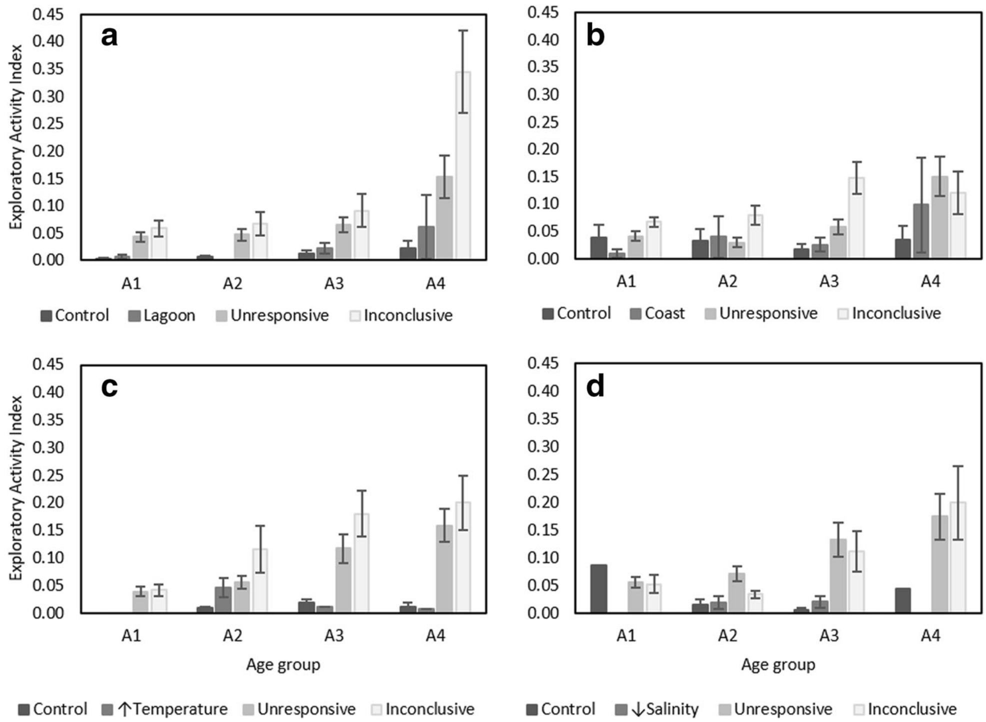


**Fig. 4** Average Exploratory Activity Index (EAI) exhibited by white seabream *Diplodus sargus* (Linnaeus, 1758) larvae in choice-chamber experiments separated by different behaviours (control water preference, stimulus water preference, unresponsive or inconclusive behaviour) in different habitat conditions (**a** test I, lagoon cue; **b** test II, coastal cue; **c** test III, increase of temperature; and **d** test IV, decrease of salinity) and across ontogeny (age 1– 22–26 DPH—days post-hatching; age 2– 32–36 DPH; age 3– 42–46 DPH; and age 4– 52–56 DPH). The error bars represent the standard deviation

**Table 6** Results of the linear mixed-effect models applied to evaluate the effects of the stimulus (test I-lagoon cue, test II-coastal cue, test III-increase of temperature and test IV-decrease of salinity) on white seabream *Diplodus sargus* (Linnaeus, 1758) larval behaviour along ontogeny (age 1– 22–26 DPH—days post-hatching, age 2– 32–36 DPH, age 3– 42–46 DPH, and age 4– 52–56 DPH) using Exploratory Activity Index (EAI) as response variable. β: estimated beta effects, $\sigma^2$: estimated variance, SE: standard error, df: degrees of freedom, *p*: significance. Significant results and tendencies are highlighted in italics

| Stimulus | Model components | Estimate | SE | df | *t* | *p* |
|---|---|---|---|---|---|---|
| Lagoon cue | *Fixed effects* | *B* | | | | |
| | Intercept | 0.037 | 0.015 | 121.5 | 2.43 | *0.016* |
| | Age 2 | 0.007 | 0.020 | 109.4 | 0.36 | 0.718 |
| | Age 3 | 0.023 | 0.021 | 121.6 | 1.06 | 0.287 |
| | Age 4 | 0.105 | 0.024 | 117.9 | 4.35 | *< 0.0001* |
| | *Random effects* | $\sigma^2$ | | | | |
| | Intercept (among-individual) | 0.003 | | | | |
| | Residual (within-individual) | 0.006 | | | | |
| | Repeatability | 0.35 | 0.133 | | | *< 0.0001* |
| Coastal cue | *Fixed effects* | *β* | | | | |
| | Intercept | 0.040 | 0.016 | 123.5 | 2.44 | *0.016* |
| | Age 2 | − 0.002 | 0.021 | 110.8 | − 0.12 | 0.899 |
| | Age 3 | 0.002 | 0.022 | 123.7 | 0.10 | 0.919 |
| | Age 4 | 0.084 | 0.024 | 122.6 | 3.48 | *< 0.0001* |
| | *Random effects* | $\sigma^2$ | | | | |
| | Intercept (among-individual) | 0.003 | | | | |
| | Residual (within-individual) | 0.005 | | | | |
| | Repeatability | 0.37 | 0.124 | | | *< 0.0001* |
| Increase of temperature | *Fixed effects* | *B* | | | | |
| | Intercept | 0.043 | 0.019 | 88.8 | 2.16 | *0.033* |
| | Age 2 | 0.018 | 0.022 | 61.7 | 0.80 | 0.424 |
| | Age 3 | 0.041 | 0.024 | 82.7 | 1.68 | *0.094* |
| | Age 4 | 0.091 | 0.026 | 79.0 | 3.44 | *< 0.0001* |
| | *Random effects* | $\sigma^2$ | | | | |
| | Intercept (among-individual) | 0.006 | | | | |
| | Residual (within-individual) | 0.003 | | | | |
| | Repeatability | 0.62 | 0.101 | | | *< 0.0001* |
| Decrease of salinity | *Fixed effects* | *β* | | | | |
| | Intercept | 0.053 | 0.034 | 97.9 | 1.57 | 0.119 |
| | Age 2 | 0.004 | 0.043 | 89.2 | 0.10 | 0.921 |
| | Age 3 | 0.066 | 0.044 | 97.5 | 1.47 | 0.142 |
| | Age 4 | 0.136 | 0.047 | 97.3 | 2.89 | *0.004* |
| | *Random effects* | $\sigma^2$ | | | | |
| | Intercept (among-individual) | 0.006 | | | | |
| | Residual (within-individual) | 0.019 | | | | |
| | Repeatability | 0.24 | 0.149 | | | *0.028* |

**Table 7** Individual-based repeatability ($R_{ICC}$) of the Exploratory Activity Index (EAI) exhibited by white seabream *Diplodus sargus* (Linnaeus, 1758) across tests performed in choice-chamber experiments (test I-lagoon cue, test II-coastal cue, test III-increase of temperature and test IV-decrease of salinity) in relation to ontogeny: age 1 (22–26 DPH—days post-hatching), age 2 (32–36 DPH), age 3 (42–46 DPH) and age 4 (52–56 DPH). SE: standard error, CI: confidence intervals, *p*: significance. Significant results are highlighted in italics

| Age | Repeatability | SE | ± 95% CI | *p* |
|---|---|---|---|---|
| Age 1 | 0.310 | 0.092 | 0.143–0.498 | *< 0.0001* |
| Age 2 | 0.304 | 0.086 | 0.137–0.478 | *< 0.0001* |
| Age 3 | 0.446 | 0.087 | 0.268–0.601 | *< 0.0001* |
| Age 4 | 0.716 | 0.070 | 0.555–0.830 | *< 0.0001* |

2016). For example, a given stimulus can increase the propensity for risk-taking behaviours by engaging in exploratory behaviour.

Personality traits may modulate the response of individuals to ecological challenges and settlement into a suitable habitat (Wolf and Weissing 2012; Canestrelli et al. 2016). Activity and exploration may affect dispersal in all developmental stages (Cote et al. 2010). Proactive individuals (i.e. more active, exploratory, and bold) have more propensity to take risks (Koolhaas et al. 1999; Coppens et al. 2010; Hall et al. 2015) and consequently better ability to acquire food and avoid predators that are determinants for growth, survival and dispersal (Cote et al. 2010; Jørgensen et al. 2013; Dall and Griffith 2014; Nanninga and Berumen, 2014). Indeed, the influence of personality traits on dispersal strategies has been suggested to affect the direction and distance of larval dispersion (Sundelöf and Jonsson 2012).

Currently, the consequences of individual behavioural consistency of white seabream larvae on dispersal, or of any other temperate fish larvae hatching from pelagic eggs, remain unknown. Based on our results, we propose that the increase in exploratory activity across ontogeny may diminish random dispersion of white seabream larvae.

## Conclusions

Contrary to our hypotheses, white seabream larvae did not show a preference for either lagoon or rocky shore habitat cues, neither towards increased water temperature or decreased water salinity. However, exploratory activity increased during ontogeny. Importantly, we demonstrated for the first time that personality traits of a temperate fish larvae hatched from pelagic eggs are present very early in ontogeny with high short-term repeatability and independently of the presented stimulus. We also observed that exploratory activity was higher when larvae showed unresponsive or inconclusive behaviours, meaning that larvae were possibly trying to find different stimuli than those that were offered (unresponsive behaviour) or just showed a random habitat selection (inconclusive behaviour). Thus, personality traits could influence the process of searching for suitable nursery habitats and, consequently, dispersion and connectivity of white seabream populations. Ultimately, characterizing the behaviour of temperate pelagic marine fish larvae and understanding active habitat selection may increase our understanding of recruitment variability, refine larval dispersal models and add to the body of knowledge on the effects of environmental and global changes and habitat degradation on fish distribution.

**Acknowledgements** The authors would like to thank the colleagues from Estação Piloto de Piscicultura de Olhão (EPPO)/Aquaculture Research Station–Instituto Português do Mar e da Atmosfera (IPMA, Portugal), especially to Marisa Barata and Tetyana Urshulyak. We are very grateful to one anonymous reviewer and Petri Niemela for very helpful and constructive suggestions on data analyses.

**Funding information** This study received Portuguese national funds from FCT—Foundation for Science and Technology through project UID/Multi/04326/2019, CLIMFISH project—A framework for assess vulnerability of coastal fisheries to climate change in Portuguese coast founded by Portugal 2020, n2/SAICT/2017—SAICT (Projetos de IC&DT) and DIVERSIAQUA project (Mar2020 16-02-01-FMP-0066). VB was funded by FCT—Foundation for Science and Technology with a Ph.D. fellowship (SFRH/BD/104209/2014). FL was funded by FCT—Foundation for Science and Technology in the ambit of the contract program DL57/2016/CP1361/CT0008.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All the experiments were conducted in accordance with the Guidelines of the European Union Council (86/609/EU) and Portuguese legislation for the use of laboratory animals and enforced by CCMAR. CCMAR staff are certified to house and conduct experiments with live animals, and their facilities are also certified in accordance with the three "R" policy, national and European legislation, and with guidelines defined by the ethical committee ORBEA CCMAR-CBMR.

**Ethical statement** This manuscript is all original work, has not been published previously (partially or in full). No data in this manuscript have been fabricated or manipulated, and all authors have given consent to submit this manuscript and have contributed sufficiently to the scientific work.

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