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Consistency in European seabass coping styles: A life-history approach

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ABSTRACT

Recent years have seen a growth of interest in the consistent differences in individual behaviour over time and contexts constituting the so-called "individual coping styles". An understanding of this inter-individual variation is essential to improve our knowledge of the adaptive value of behaviour. Coping styles may have implications in diverse fields, so the development of appropriate screening methods for each species appears to be the most effective way to extend our knowledge and to incorporate behavioural responses into selection-based breeding programmes, to improve the domestication and welfare of farmed fish. We tested 30 juvenile seabass (*Dicentrarchus labrax*) at least twice in individual-based tests (feeding recovery in isolation, aggressiveness, exploration in a T-maze and net restraint) and group-based tests (risk-taking and hypoxia sorting), to assess coping style consistency in the short- and long-term and between tests. The results of individual-based tests were inconsistent over time and between tests in our setup: the time between repeat tests, learning and species-specific behavioural responses appeared to have a major impact. By contrast, the results of group-based tests, such as risk-taking and hypoxia sorting, appeared to be consistent (both in the short- and long-term). These tests therefore appeared to be the most relevant for the characterisation of coping style in European seabass. Furthermore, the results of these tests were also predictive of cortisol stress response. These tests are simple to perform and can be used to screen large numbers of fish, the first step in selection programmes including behavioural profiles.

1. Introduction

There has been an increase in interest in the consistent differences in individual behaviour over time and contexts. Consistency is the predictability of repeated measurements for the same individuals and it can be used to provide estimates for populations (Nunnally, 1967; Réale et al., 2007). It has been clearly shown that, within species (vertebrates or invertebrates), individuals may react differently to the same situation. This individual variability is generated by a collection of correlated physiological and behavioural responses, known as the coping strategy or coping style (Koolhaas et al., 1999). Various behavioural models reflecting coping strategies exist for mammals,

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birds and teleosts (cichlids, salmonids, sticklebacks and a large number of tropical fish, reviewed in Øverli et al., 2007). Individuals with divergent coping styles can be clustered into two main categories: proactive and reactive individuals. Proactive individuals tend to engage in active avoidance or cope with stressful stimuli (Koolhaas et al., 1999; Koolhaas, 2008) through a "fight or flight" response. Their behaviour differs from that of reactive individuals as follows: (1) they are more aggressive/dominant (Øverli et al., 2004; Castanheira et al., 2013a), (2) they show greater motivation to feed after transfer to a novel environment (Øverli et al., 2007), (3) they rapidly approach new objects (Castanheira et al., 2013b), (4) they take more risks (i.e. they are bolder) and are more likely to explore when exposed to novelty (Øverli et al., 2006; MacKenzie et al., 2009; Martins et al., 2011a) and (5) they tend to develop behavioural routine (Bolhuis et al., 2004; Ruiz-Gomez et al., 2011). Physiologically, a proactive strategy is associated with lower hypothalamus–pituitary–interrenal (HPI) activity (de Boer et al., 1990; Øverli et al., 2005, 2007; Silva et al., 2010) and higher sympathetic reactivity (Øverli et al., 2007) than in reactive individuals. Therefore, proactive animals typically have lower basal concentrations of glucocorticoids (the principal hormones involved in the stress response and the ultimate product of HPI axis activation) and lower stress-induced glucocorticoids concentrations (Øverli et al., 2007) than reactive individuals. As individuals differ in their behavioural and physiological responses, they probably display differential adaptation to different types of environment.

An understanding of this individual variation is essential to increase our knowledge of the adaptive value of behaviour (Wolf et al., 2007), which may affect individual fitness. Moreover, coping style has been shown to have implications in a wide range of fields (reviewed by Castanheira et al., 2013b) including behavioural ecology (Réale et al., 2007), neurosciences (Veenema et al., 2003), aquaculture (Huntingford and Adams, 2005), welfare (Øverli et al., 2004), health and susceptibility to disease (Fevolden et al., 1993; Koolhaas, 2008), performance traits (Martins et al., 2011b) and interpretations of molecular responses (MacKenzie et al., 2009). In addition, several studies have demonstrated the existence of QTL associated with boldness and stress responses (Benus et al., 1991; Dingemanse et al., 2002; van Oers et al., 2004; Wright et al., 2006; Dingemanse et al., 2012; Rexroad et al., 2012), suggesting that it may be possible to select individuals on the basis of coping style.

Several methodological approaches have been used to characterise coping styles in fish. The methods used have included individual-based tests, such as confinement in rainbow trout (*Oncorhynchus mykiss*) (Øverli et al., 2004, 2007), recovery of feeding motivation in a novel environment in African catfish (*Clarias gariepinus*) (Martins et al., 2005) and rainbow trout (Øverli et al., 2007), Senegalese sole (*Solea senegalensis*) (Silva et al., 2010) and Nile tilapia (*Oreochromis niloticus*) (Martins et al., 2011c), exposure to a novel object in Nile tilapia (Martins et al., 2011c), aggression tests in rainbow trout (Øverli et al., 2007) and gilthead seabream (*Sparus aurata*) (Castanheira et al., 2013a), and restraint tests in Senegalese sole (Silva et al., 2010; Martins et al., 2011a) and gilthead seabream (Arends et al., 1999; Castanheira et al., 2013a). Most of these behavioural tests are carried out in isolation conditions, but the gregarious character of certain species may influence behavioural responses and should be taken into account when interpreting data (reviewed by Ashley, 2006). Some group-based tests have also been developed. Most of these tests concern risk-taking in European seabass (*Dicentrarchus labrax*) (Millot et al., 2009) or common carp (*Cyprinus carpio*) (Huntingford et al., 2010) and hypoxia exposure in rainbow trout (Laursen et al., 2011) and gilthead seabream (Castanheira et al., 2013b).

Most behavioural studies assessing the consistency of coping style over time are based on the use of different tests over a relatively short period (e.g. tests were repeated over 1 week by Budaev et al., 1999 or 2 weeks by Castanheira et al., 2013b). Analyses of the consistency of behavioural screening results between repeated tests or different challenges (cross-context analyses) are generally carried out over periods of 1–8 days (Wilson and Stevens, 2005; Øverli et al., 2007; Wilson and Godin, 2009; Wilson et al., 2010). Few studies have investigated the repeatability of personality tests over both short and long intervals (see David et al., 2012). However, Bell et al. (2009) reported that repeatability was generally greater for experiments separated by short intervals than for those separated by longer intervals. This is not surprising, because several studies have indicated a role for various factors in shaping or influencing coping style. These factors include predation pressure (Brown and Braithwaite, 2004; Brown et al., 2005; Archard and Braithwaite, 2011; Archard et al., 2012), the predictability of food supply (Chapman et al., 2010) and food density (Dunbrack et al., 1996), social interactions (Chapman et al., 2008), temperature or hypoxia (Biro et al., 2010), learning (Millot et al., 2009), environment stability (Brelin et al., 2008) and stress (Ruiz-Gomez et al., 2008). Stamps and Groothuis (2010) pointed out that behavioural tendencies that are consistent over short periods of time are likely to change over longer periods. Researchers must therefore consider carefully the observation intervals most appropriate for their focus species and for the questions addressed. We therefore decided to use a life-history approach in our species of interest, seabass, a marine fish of particularly high commercial value, with a current mean European production of about 125,000 metric tonnes year^{-1} (Tveteras and Nystoyl, 2011).

The aim of this study was to assess individual coping style through the use of various individual-based and group-based tests, adding a life-history approach to data interpretation. The chosen approach was the screening of individually tagged fish in repeated (at least twice) tests over a long period (629 days, from 129 to 758 days post-hatching, dph), with the use of various intervals between tests. The aims were: (i) to assess behavioural and physiological consistency over time, (ii) to define the most appropriate test for the characterisation of coping style in seabass and (iii) to determine the most appropriate time interval between tests if repetition is needed. This approach made it possible to assess various aspects of individual behavioural consistency and to evaluate age and life experience effects. By using different tests, we were also able to