Coping styles in farmed fish: consequences for aquaculture

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Abstract :

Individual differences in physiological and behavioural responses to stressors are increasingly recognised as adaptive variation and thus raw material for evolution and fish farming improvements including selective breeding. Such individual variation has been evolutionarily conserved and is present in all vertebrate taxa including fish. In farmed animals, the interest in consistent trait associations, that is coping styles, has increased dramatically over the last years because many studies have demonstrated links to performance traits, health and disease susceptibility and welfare. This study will review (i) the main behavioural, neuroendocrine, cognitive and emotional differences between reactive and proactive coping styles in farmed fish; (ii) the methodological approaches used to identify coping styles in farmed fish, including individual (group) mass-screening tests; and (iii) how knowledge on coping styles may contribute to improved sustainability of the aquaculture industry, including welfare and performance of farmed fish. Moreover, we will suggest areas for future research, where genetic basis (heritability/epigenetic) of coping styles, and the neuroendocrine mechanisms behind consistent as well as flexible behavioural patterns are pinpointed as central themes. In addition, the ontogeny of coping styles and the influence of age, social context and environmental change in coping styles will also be discussed.

Keywords : behavioural syndromes, farm animals, individual variation, personality, stress response

64 **Introduction**

65 In animals, including fish, individual differences in response to challenges are associated with

66 differences in behaviour (Øverli *et al.* 2007; Réale *et al.* 2010). Many of these associations have

67 been shown to be consistent under stressful conditions and thus to represent coping styles in

68 accordance with the definition by Koolhaas *et al.* (1999), as *a coherent set of behavioural and*

69 *physiological stress responses, which is consistent over time and which is characteristic to a*

70 *certain group of individuals'*. Terminology remains one of the main challenges when

71 addressing the topic of consistent individual variation in physiology and behaviour. Other

72 authors use terms such as behavioural syndromes (Sih *et al.* 2004), personality (Gosling 2001)

73 and temperament (Francis 1990) more or less synonymously, while physiologists tend to refer

74 to coping styles. These terms and designated definitions, share common grounds such as the

75 recognition that individual variation may be consistent and biologically meaningful, and

76 individual differences in certain behavioural traits are consistent and predictive of other

77 behaviours or physiological responses shown in another context. Typically, in biomedical

78 research and agricultural sciences the term ―coping styles" is preferred, while in behavioural

79 ecology the terms behavioural syndromes are more common. The range of biological

80 parameters considered also differs between the different terms. Coping styles often include both

81 behavioural and physiological responses to unfavourable environments and stress (Koolhaas *et*

82 *al.* 1999) while behavioural syndromes include only behavioural differences and not necessarily

83 under stress conditions. Personality and temperament, in humans, include essentially emotional

84 reactivity traits. However, when applied to animals, the term personality often ignores the

85 emotional component. Table 1 summarises the terminology concerning individual variation.

86 Recognising that both physiological and behavioural traits are important, throughout this review

87 the term ―Coping styles" will be used in accordance with the definition by Koolhaas *et al.*

88 (1999, see above).

89 In fish, the importance of understanding mechanisms involved in coping styles have gained

90 increasing attention. Especially since, conditions that are well tolerated by some individuals

91 may be detrimental to others, the concept of coping styles are important for their welfare

92 (Huntingford & Adams 2005; Huntingford *et al.* 2006), health and diseases resistance (Fevolden

93 *et al.* 1992,1993; MacKenzie *et al.* 2009, Kittilsen *et al.* 2012), performance traits (Martins

94 2005, Martins *et al.* 2011b; Øverli *et al.* 2006 ab) and interpretations of molecular data

95 (Johansen *et al.* 2012; MacKenzie *et al.* 2009; Rey *et al.* 2013).

96 Moreover, Martins *et al* (2011b) showed that coping styles are predictive of how stimuli are

97 appraised, supporting the inclusion of emotional or affective states (in this case fear) as essential

98 component of coping styles in fish. Also Millot *et al* (2014a) shown that fish are able to retain

99 memories of events with positive/negative valence which are retrieved by environmental cues.

100 Table 2 summarises the main behavioural and physiological differences between reactive and

101 proactive individuals. Nevertheless, it is imperative to note that the differentiation in coping

102 styles may not be expressed as a binomial distribution in most of the species but rather as a

103 continuous distribution with the majority of individuals expressing intermediate characteristics.

104 In addition, Boersma (2011) suggested that the relative occurrence of contrasting coping styles

105 depends on the type of population (i.e. wild or domesticated). This author showed that in wild

106 populations of rats, the coping strategies of the individuals within a population display a

107 binomial distribution: with extremes proactive vs. reactive individuals. Rats with an

108 intermediate coping style are generally not present in a population in the wild since they have a

109 lower fitness in both stable and new or instable environments. In contrast, Réale *et al.* (2007,

110 2010 ab) demonstrated a normal distribution of coping styles in the wild in several species.

111 Moreover, in laboratory or domestic settings there is less environmental pressure pushing the

112 population into a bimodal distribution of coping styles. This means that in domesticated

113 population a normal distribution in coping styles is usually observed (Spoolder *et al.* 1996).

114 Nowadays, stress coping styles are clearly identified in fish and have contributed to the

115 understanding of individual variation in the ability to cope with stressful events. A consensus is

116 emerging that increased understanding of the consequences of stress coping styles in

117 aquaculture is important to safeguard a sustainable development of this industry.

118

119   This study will review: 1) the main behavioural, neuroendocrine, cognitive and emotional

120   differences between reactive and proactive coping styles in farmed fish, 2) the methodological

121   approaches used to identify coping styles in farmed fish; including individual (group) mass-

122   screening tests and 3) how knowledge on coping styles may contribute to improved

123   sustainability of the aquaculture industry, including welfare and performance of farmed fish.

124

125   **Assessment of coping styles in farmed animals**

126   *Land farm animals*

127   Assessment of coping styles in farm animals gained momentum in the late 1980´s. In those

128   studies researchers applied the concept of coping styles to domestic livestock and started to

129   understand how distinct individual traits were related with stress coping under common rearing

130   conditions. For instance, in piglets, the most common test is the ―back test" (Hessing *et al.*

131   1993,1994) which consists of restraining each piglet in a supine position for 1 min and

132   classification of pigs is then based on the number of escape attempts made. Other tests

133   commonly used in pigs and other farm animals like cows, cattle and sheep are the open field test

134   (Spoolder *et al.* 1996; Magnani *et al.* 2012 ; Van Reenen *et al.* 2005), the novel object test

135   (Spoolder *et al.* 1996; Magnani *et al.* 2012; Spake *et al.* 2012; Van Reenen *et al.* 2005), the

136   novel environment test (Hopster, 1998) and the resident intruder test (Bolhuis *et al.* 2005a;

137   Spake *et al.* 2012). Along with behavioural responses also physiological responses are measured

138   including cortisol responsiveness, heart rate (Korte *et al.* 1999), gastric ulceration and

139   vocalisation (Hessing *et al.* 1993; Ruis *et al.* 2001; Van Reenen *et al.* 2002; van Erp-van der

140   Kooij *et al.* 2003; Van Reenen *et al.* 2005; Hopster, 1998; Spake *et al.* 2012).

141   Several traits attributed to proactive and reactive individuals in land farmed animals have also

142   been identified in fish suggesting that many of such traits have been evolutionary conserved in

143   vertebrates (see references below).

144

145

146

147   *Identifying coping styles in farmed fish*

148   Over the last years, the number of papers addressing coping styles in fish has raised rapidly.

149   Many of these studies address farmed fish including common carp (*Cyprinus carpio*)

150   (MacKenzie *et al.* 2009; Huntingford *et al.* 2010), Nile tilapia (Barreto & Volpato 2011;

151   Martins *et al.* 2011bd), Atlantic salmon (*Salmo salar*) (Kittilsen *et al.* 2009a, 2012; Vaz-Serrano

152   *et al.* 2011), Atlantic halibut (*Hippoglossus hippoglossus*) (Kristiansen & Fernö 2007), rainbow

153   trout (Øverli *et al.* 2005, 2006ab; Schjolden *et al.* 2005; Ruiz-Gomez *et al.* 2008, 2011;

154   Höglund *et et al.* 2008; Laursen *et al.* 2011)), sea bass (Millot *et al*. 2009 ab) and gilthead

155   seabream (Castanheira *et al*. 2013ab; Herrera *et al.* 2014) Table 2.

156   Like in mammals, two main coping styles are typically recognised: proactive (active coping or

157   bold or ‗fight-flight') and reactive (passive coping or shy or ‗non-aggressive').

158   Typically, proactive individuals are behaviourally characterized by: 1) active escape from a

159   stressor (Brelin *et al.* 2005; Laursen *et al.* 201; Silva *et al.* 2010; Martins *et al.* 2011c); 2) high

160   feed efficiency (Martins *et al.* 2005ab, 2006ab; van de Nieuwegiessen *et al.* 2008); 3) high

161   feeding motivation after transfer to a new environment (Øverli *et al.* 2007) or food type

162   (Kristiansen & Fernö 2007); 4) high risk taking and exploratory when exposed to novelty

163   (Huntingford *et al.* 2010; Øverli *et al.* 2006a; MacKenzie *et al.* 2009; Millot *et al.* 2009a); 5)

164   high social rank (dominant) during aggressive encounters (Øverli *et al.* 2004, 2005; Castanheira

165   *et al.* 2013a); 6) low social influence (Magnhagen, 2007; Magnhagen & Staffan 2005;

166   Magnhagen & Bunnefeld, 2009); 7) low sensitive to environmental stressors (Höglund *et al.*

167   2008); 8) establishment of routines and have less behavioural flexibility (Chapman *et al.* 2010;

168   Ruiz-Gomez *et al.* 2011) when compared to reactive individuals. Proactive individuals exhibit

169   typical physiological and neuroendocrine characteristics such as: 1) lower hypothalamus-

170   pituitary-interrenal (HPI) activity (Silva *et al.* 2010), as measured by basal cortisol levels; 2)

171   lower HPI reactivity (Castanheira *et al.* 2013a; Øverli *et al.* 2007; Trenzado *et al.* 2003), as

172   measured by increase in cortisol over basal levels when stressed; 3) higher sympathetic

173   reactivity and lower parasympathetic reactivity (Verbeek *et al.* 2008; Barreto & Volpato 2011),

174   measured as opercular beat rate; 4) low hormonal modulation (LeBlanc *et al.* 2012); 5) higher

175   oxygen consumption during stress (Herrera *et al.* 2014; Killen *et al.* 2011; Martins *et al.* 2011c);

176   6) lower myocardial dysfunction (Johansen *et al.* 2011); 7) lower neural plasticity (Johansen *et*

177   *al.* 2012) and 8) high immunity (Kittilsen *et al.* 2012) when compared to reactive individuals.

178   In addition to behaviour, physiological and neuroendocrine characteristics, proactive and

179   reactive fish have also been reported to differ in cognitive and emotional traits. One of the best

180   examples of the characterization of coping styles in fish comes from studies using selected lines

181   of rainbow trout (*Oncorhynchus mykiss*). These lines were segregated into high- and low-

182   responding individuals (HR, LR) on the basis of their plasma cortisol response after

183   confinement test (Pottinger & Carrick 1999). Studies in these lines demonstrated a link between

184   cognition and coping styles: Moreira *et al.* (2004) showed that HR-LR individuals differed in

185   memory retention in addition to cortisol responsiveness. The extinction of a conditioned

186   response (i.e. how quickly the conditioned response was lost after the end of reinforcement) was

187   greater among LR individuals.

188   In accordance with this, Ruiz-Gomez *et al.* (2011) showed a higher propensity to develop and

189   follow routines (reversal learning) in LR trout. They continue to perform a learned pattern even

190   if the conditions change. LR fish showed slower reversal learning when finding relocated feed,

191   and it was suggested that this reflects a cognitive difference, where LR fish have a stronger

192   tendency to develop and follow routines. This is in accordance with what have been suggested

193   as general differences between proactive and reactive individuals, where reactive individuals

194   react to environmental changes while proactive individuals follow predictions of the actual

195   environment (Coppens *et al.* 2010).

196   Various methodologies used to characterise coping styles in fish have been adapted from those

197   used in land farmed animals, an example is the restraining test, which is very similar to the

198   back-test commonly used in pigs. The restraining test in fish consists of holding each individual

199   in an emerged net for a certain limited period depending on the species (Arends *et al.* 1999;

200   Silva *et al.* 2010; Castanheira *et al.* 2013 ab). While in the net, the following behaviours have

201   been measured: latency to escape, number of escape attempts and total time spent on escape

202   attempts. Proactive individuals have been shown to exhibit more and longer escape attempts as

203 compared to reactive individuals (Silva *et al.* 2010; Martins *et al.* 2011ac). Other tests used in

204 land farmed animals that have been adapted and applied to fish include the novel object test

205 (Frost *et al.* 2007; Basic *et al.* 2012), the exploration test (Chapman *et al.* 2010; Killen *et al.*

206 2011; Magnhagen & Staffan 2005; Magnhagen & Bunnefeld 2009 and the resident intruder test

207 (Øverli *et al.* 2002ab; Brelin *et al.* 2005).

208 Recent studies using farmed fish as models have suggested the possibility to discriminate

209 coping styles using grouped-based test (e.g. hypoxia test developed in rainbow trout by Laursen

210 *et al.* (2011) and adapted to gilthead seabream by Castanheira *et al.* 2013b). Briefly, the hypoxia

211 test consists of reducing the oxygen levels in one side of a two chambers tank and measuring the

212 escape behaviour from the hypoxia to the normoxia side. Another group-based test is the risk-

213 taking test (or exploration test) which consists of a tank separated in two distinct areas: safe and

214 risk areas. Fish are placed in the safe area (darkened settling chamber), connected by a plastic

215 tunnel or an opening to a risk area (open field). The risk area is usually associated to feed

216 delivery zone to stimulate fish going to the non-familiar area (Millot *et al*. 2009; Huntingford *et*

217 *al.* 2010; Castanheira *et al.* 2013b).

218 Finally, it should be noted that an increasing number of studies also report that contrasting

219 coping styles in fish are reflected in somatic and morphological traits such as developmental

220 rate (Andersson *et al.* 2011, 2013ab) and pigmentation patterns (Kittilsen et al., 2009ab, 2012;

221 Bäckström *et al.* 2014). Genetic markers for variable stress resistance are also increasingly

222 explored (Rexroad et al., 2012). Thus, tools to characterise coping styles and personality traits

223 in fish are becoming increasingly available which fulfils an important prerequisite for the effort

224 towards understanding both the biological background and applied potential of this type of

225 individual variation.

226 The presence of coping styles in the most important farmed fish species and the common tests

227 used are presented in Table 3.

228

229

230 **Consistency and plasticity of coping styles in farmed fish**

231 One of the major gaps in the literature concerning the characterization of coping styles in

232 animals, including fish, is the lack of knowledge on the consistency of individual differences.

233 This includes knowledge on both contextual consistency i.e. _the extent to which scores for

234 *behaviour expressed in one context are correlated across individuals with scores for behaviour*

235 *expressed in one or more other contexts, when behaviour in all of the contexts is measured at*

236 *the same age and time* and temporal consistency i.e. _the extent to which scores for behaviour

237 *in a given context at a given time are correlated across individuals with scores for the same*

238 *behaviour in the same context at a later time* (Stamps & Groothuis 2010).

239 Studies in the HR/LR rainbow trout lines showed that proactive and reactive individuals exhibit

240 consistent traits. Over a period of 7 days, feeding responses after transfer into a novel

241 environment, responses to a novel object, aggressiveness and responses to confinement were

242 behaviourally constant, but no differences between lines were apparent (Basic *et al.* 2012). The

243 ontogenic consistency of these traits where also demonstrate by Höglund *et al*. (2008) and

244 Andersson *et al.* (2011, 2013ab).

245 However, most of the studies on coping styles characterization have been done on selected HR -

246 LR fish lines (Øverli *et al.* 2005, 2007) which raises the question whether similar consistency

247 responses can be observed in non-selected populations. In line with the previous information,

248 recent studies on non-selected populations seem to support the consistency of behavioural

249 responses both over time and across-context. Castanheira *et al*. (2013b) using a non-selected

250 population of gilthead seabream (*Sparus aurata*) showed that individual differences in risk-

251 taking behaviour and escaping behaviour in response to stressors are consistent over a period of

252 15 days. Moreover the same authors also showed that some behaviour can be used to predict

253 other behaviours expressed in a different context (e.g. individuals that took longer to recover

254 feed intake after transfer into a novel environment, exhibited higher escape attempts during a

255 restraining test and escaped faster from hypoxia conditions).

256 Consistency of individual differences is a key element to identify coping styles in fish.

257 However, this does not exclude the possibility that individuals change their coping style over

258 time and context. In fact individual plasticity i.e. _the extent to which the behaviour expressed

259 by individuals with a given genotype in a given context at a given age and time varies as a

260 function of the set of conditions experienced by those individuals before the behaviour was

261 expressed' (Stamps & Groothuis 2010), is very important because it allows individuals to adjust

262 their behaviour to novel or instable environments. Few studies have addressed how plastic,

263 proactive and reactive coping styles are. Frost et al. (2007) suggested that social context is an

264 important modulator of coping styles in rainbow trout. These authors showed that bold

265 individuals observing another's losing fights or with lower responses to novelty (novel objects

266 and novel prey) reduced their boldness. However, shy individuals just alter their behaviour

267 (increase their boldness responsiveness) when their relative competitive ability was similar or

268 higher than their conspecifics. These results suggest that bold individuals may be more flexible

269 to changing conditions as opposed to shy individuals (Frost et al. 2007). Similar differences in

270 behavioural plasticity have been documented during feeding response in presence of the novel

271 object. Basic et al. (2012) showed that proactive individuals adopt a more flexible behaviour by

272 suppressing feed intake in presence of the novel object. In contrast, Ruiz-Gomez et al. (2011)

273 have reported opposite results, i.e. LR (proactive) individuals seem to be more fixed in

274 responses (relocated feed) when confronted with a new situation in contrast with HR

275 individuals.

276 Individuals differ in how the environmental stimuli are appraised and how they are able to

277 adjust and adapt their physiology and behaviour to help them cope more effectively. Part of this

278 plasticity is supported and influenced by cognition and neural plasticity. The underlying

279 neurobiological mechanism underpinning differences in plasticity between reactive and

280 proactive individuals have been recently studied by Johansen et al. (2012) in the HR/LR

281 rainbow trout lines. These authors measured genes involved in neural plasticity and

282 neurogenesis (PCNA, BDNF, NeuroD and DCX) using quantitative PCR in brains of rainbow

283 trout under baseline conditions and in response to short-term confinement and long-term social

284 stress. They showed that a higher degree of neural plasticity in reactive individuals might

285 provide the ideal conditions to support their higher behavioural flexibility as opposed to

286 proactive individuals.

287 Furthermore, Ebbesson & Braithwaite (2012) reviewed the influence of neural plasticity and

288 cognition shaped by the environmental experiences in several fish species. These authors agree

289 that, neural plasticity aids in the adaptation and flexibility, demanding by the diverse

290 environments in which fishes live. These, make the brain more sensitive to the surrounding

291 environment moulding the adaptive responses to the environment both over the individual life

292 and over evolutionary time.

293 However, there is still a long way to go in understanding plasticity of coping styles in order to

294 improve the management and welfare of aquaculture populations.

295 Aspects of how coping styles change with age, social context and new environmental conditions

296 should be explored in the future. Environmental changes might be particularly relevant during

297 this era of an ongoing global climate change. Global warming could cause changes in species

298 behaviour and life history (Kling *et al.* 2003). The impacts of climate change in aquaculture can

299 be direct e.g. changes in water temperature, or indirect such as the increase of fishmeal costs

300 and its consequences for aquaculture feeds. The recent approach by Dingemanse *et al.* (2009)

301 offers a theoretical framework to help understanding plasticity of coping styles. They proposed

302 the concept of behavioural reaction norms, i.e. measuring individual behavioural response over

303 an environmental gradient (e.g. social environment, environmental changes). According to the

304 same authors the same behaviour can be measured over multiple environmental gradients and

305 individual behaviour can be described as a linear regression line linking the response with the

306 environmental conditions. In the linear regression the intercept of the line describes the average

307 individual level of the behaviour and the slope represents the individual degree of plasticity.

308 Using temperature as an environmental gradient, on a recent work with zebrafish, Rey et al.

309 2014 (submitted) showed differences in thermal preferences for proactive and reactive fish

310 under a thermal gradient. Proactive individuals preferred higher temperatures than reactive

311 reflecting differences already detected on basal metabolic rates and different acclimation and

312 environmental adaptation capacities between both coping styles.

313   *Proxies for measuring coping styles in fish*

314   Coping styles characterization in fish can be time consuming, especially when individual-based

315   tests are used. Therefore, several proxies have been suggested in the literature to characterize

316   coping styles without the need to undertake complex behavioural tests.

317   Ventilation rate has been shown to be a sensitive indicator of fish physiological responses to

318   stress. Barreto & Volpato (2011) observed that ventilation rates of Nile tilapia were correlated

319   with the feeding resumption in isolation. Individuals with high ventilation rates resumed feeding

320   later than fish with low ventilation rates.

321   Skin pigmentation has also been suggested to predict coping styles in fish (Kittilsen *et al.* 2009

322   ab; 2012). High spotted Salmonids showed lower cortisol levels than lower spotted conspecifics

323   (Figure 1). Visual markers provide a suitable tool that can be easily combined with other

324   common procedures, such as size-grading or vaccination. Furthermore, Kittilsen *et al.* (2012)

325   provided evidence for individual variation in parasites incidences while screening distinct

326   coping styles. Individuals with high incidence of black skin spots harboured fewer ectoparasites

327   (sea lice) as compared to less pigmented fish.

328   Observations of ear and tail postures are reliable non-invasive method for assessing emotional

329   reactivity in pigs (Reimert *et al.* 2013) and sheep (Reefmann *et al.* 2009) and have been

330   suggested as proxies for coping styles screening. In fish very little is known about the link

331   between body postures and coping styles. Recently, Martins *et al.* (2012) used fin spreads

332   (defined as a sudden elevation of the dorsal fin) to distinguish bold and shy individuals of the

333   colonial fish, *Neolamprologus caudopunctatus*. Results showed that reactive individuals

334   exhibited a higher number of fin spreads in response to novelty.

335   The time to reach the first feeding in Salmonids has also been suggested to predict coping

336   styles. Recently, Andersson *et al.* (2013b) reported a coupling between stress coping styles and

337   the time to reach first feeding (low cortisol responders had larger yolk reserves at emergence

338   time) which can be used as a proxy.

339   **What are the consequences of different stress coping styles in farmed fish for**

340   **Aquaculture?**

341 The presence of coping styles is now well recognised in farmed fish and its implication for

342 aquaculture can be widespread. Individual fish within a population often differ in how strongly

343 they respond, behaviourally and physiologically, under stress conditions. A failure to

344 accommodate the coping styles of fish under farming conditions can lead to problems linked

345 with production (e.g. aggression, growth and disease resistance).

346

347 *Growth performance and energetics*

348 One of the best examples of the implications of coping styles in performance traits comes from

349 studies with African catfish (Martins 2005). By studying individual differences in growth and

350 how these relate with individual differences in feed intake, feeding behaviour and feed

351 efficiency, Martins (2005) showed that the most efficient individuals were those reacting

352 quicker to the presence of pellets and consuming their meals faster after transfer into a novel

353 environment. These individuals were also those that exhibited a lower cortisol response after

354 acute stress. All these characteristics (better feed efficiency and lower stress responsiveness) are

355 clearly beneficial under aquaculture conditions.

356 Several studies revealed that coping styles play an important role in growth performance and

357 feed conversion. In common carp the competitive ability (success in gaining access to a

358 spatially restricted feed source) was shown to be consistent over time and related to risk-taking

359 behaviour (Huntingford *et al.* 2010). The same behavioural characteristics have been observed

360 on sea bass (Millot *et al.* 2009b). Data from Martins *et al.* (2011 abd) have shown that proactive

361 individuals (*Nile tilapia*) seem to exhibit a faster recovery of feed intake after transfer and to use

362 feed resources more efficiently. In Atlantic salmon conditions that normally prevail in intensive

363 rearing systems (e.g. restricted feeding regimes, high density) may favour proactive individuals

364 (Huntingford 2004; Huntingford & Adams 2005).

365 Coping styles have also been linked with differences in metabolism (Huntingford *et al.* 2010;

366 Martins *et al.* 2011c). In nature, the metabolic rate of an animal is linked to the willingness of

367 risk-taking while foraging (Careau *et al.* 2008). Hence, increased energetic requirements in

368 individuals with a higher metabolic demand could require them to forage more often or take

more risks to achieve a higher rate of feed intake (Abrahams & Sutterlin 1999; Finstad *et al.* 2007). Huntingford *et al.* (2010) and Herrera *et al.* (2014) reported that in carp and seabream respectively the risk-taking behavioural phenotype is associated with a relatively high metabolic rate, while the risk-avoiding phenotype is associated with a lower rate. Killen *et al.* (2011) reported in sea bass that the amount of risk-taking among individuals was positively correlated with their routine metabolic rate. However, Martins *et al.* (2011c) have reported opposite results in metabolic rate (oxygen consumption) measured when Senegalese sole were housed in respirometry chambers. These authors suggested that different individuals reacted differently when housed in the metabolic chambers that functioned as confinement chambers. Individuals that consumed less oxygen in a respirometry chamber were also the individuals that reacted sooner to a confinement stress (typical from proactive coppers). This apparent contradiction may have to do with the passive benthic life-style sole, compared to other more active fish species.

In addition, yolk-sac fry originating from the HR strain were more sensitive to environmental stressors, and have shown a shorter reaction time to low oxygen levels (Höglund *et al.* 2008). This suggests that differences in coping styles are expressed at early developmental stages before social or environmental interference. Proactive individuals seem to have a ―fast" development strategy (or fast pace of life) as demonstrated by an earlier hatching and consumption of egg yolk reserves as compared to reactive (Andersson & Höglund, 2012). Such life strategy has an impact on metabolic needs and most likely on the nutritional requirements. For instance, optimal dietary lipid content could depend on coping styles because metabolic rates are different and hence energy requirements could vary.

In rats metabolic differences between coping styles have been associated with metabolic diseases (Boersma 2011). Using selected Roman Low Avoidance (RLA) and Roman High avoidance (RHA) rats Boersma (2011) showed that different strains differ in plasma insulin levels, both in baseline conditions and during the intravenous glucose tolerance tests. Reactive RLA individuals were associated with insulin resistance and elevated levels of plasma leptin,

396   free fatty acids levels, liver triglycerides, and an increased visceral fat content, especially when

397   over feeding a high fat diet. Proactive RHA individuals were extremely resistant to diet-induced

398   insulin resistance. Thus, coping styles of an individual seems to be associated with particular

399   metabolic and (patho-) physiological characteristics.

400

401   *Selection programmes*

402   Selection programmes in farmed fish focus essentially on growth performance (Gjedrem 2005).

403   As shown by Martins *et al.* (2005c) individuals exhibiting fast growth are often included in a

404   proactive coping style. However, proactive individuals have also been shown to be more

405   aggressive (Øverli *et al.* 2004; Castanheira *et al.* 2013a). Selection for fast growing individuals

406   may results in co-selection of undesirable traits such as aggression. Aggressiveness has been

407   linked with a diversity of aquaculture problems including decreased feed intake, growth

408   dispersion, chronic stress and disease vulnerability (Ashley 2007). Furthermore, fighting brings

409   a significant cost in terms of increased energy expenditure that may promote inefficient growth.

410   In addition, aggression among fish in production systems can be a cause of skin and fin damage.

411   This damage can directly reduce the value of the farmed product and increase the vulnerability

412   to diseases. Moreover, proactive individuals have also been shown to develop routines more

413   easily (Ruiz-Gomez *et al.* 2008, 2011; Basic *et al.* 2012; Frost *et al.* 2007). Such characteristic

414   may be more advantageous under stable conditions provided by intensive husbandry systems

415   but prejudicial in extensive or semi-intensive husbandry systems with lower standardized

416   conditions.

417

418   *Disease resistance and parasites*

419   Another important implication of coping styles in farmed fish is the different disease

420   susceptibility exhibited by proactive and reactive individuals. Diseases are one of the main

421   challenges in aquaculture and can represent a considerable financial burden to the farmer.

422   Studies on inflammatory challenge with bacterial pathogens reported distinct disease resistance

423   between coping styles (Fevolden *et al.* 1992, 1993; MacKenzie *et al.* 2009).

424   Fevolden *et al.* (1993) suggested selection targeting distinct coping styles rather than for

425   specific immune traits, selecting for a broad spectrum of defence mechanisms and hence

426   affecting resistance to several diseases.

427   Moreover, MacKenzie *et al.* (2009) showed distinct regulation of proinflammatory gene

428   expression suggesting that fundamental differences in cytokine regulation exist in fish with

429   distinct coping styles. In particular, tumor necrosis factor-alpha (TNFα) and interleukin 1-beta

430   (IL1β), putative cytokines involved in the development of inflammation in fish, differed

431   between proactive and reactive individuals.

432   Among the diseases, Salmon lice are considered a major threat to marine Salmonids farming

433   (Johnson *et al.* 2004) the evidence that salmon with higher black skin spots harboured fewer

434   mature female lice carrying egg sacs suggests that individual host traits may decrease parasite

435   infestation. Moreover (Øverli *et al.* 2014) demonstrate that the presence of sea lice affect

436   behaviour and brain serotonergic activity in Atlantic salmon. Still, further studies should

437   address the biology behind coping styles and resistance to parasites, bacteria and viruses.

438   Furthermore, (Kittilsen et al. 2009b) established that distinct pigmentation profiles are

439   correlated with stress cortisol response in Salmonids (Figure 1). Low cortisol responders were

440   found to be consistently more spotted than high cortisol responders. Another study by the same

441   authors Kittilsen *et al.* (2012) provided evidence for individual variation in parasites resistance

442   to sea lice particularly, salmon louse (*Lapeophtheiras salmonis*) carrying egg sacs.

443

444   *Fish welfare*

445   In most fish species, chronic or acute stress is considered as the main factor reducing animal

446   welfare in intensive husbandry productions (Ashley 2007; Huntingford *et al.* 2006). However,

447   despite the link between acute response to challenges and coping styles very little information is

448   available about chronic stressors and coping styles.

449   One of the best examples used to discriminate distinct susceptibility to chronic stressors was

450   performed using selected lines of wild house-mice. Strains of mice have been created through

451   selective breeding for divergent hypothalamic-pituitary-adrenal axis responses to a standardized

452   aggressiveness test: Short Attack Latency, high aggressive/ proactive (SAL) and Long Attack

453   Latency, low to non-aggressive/ reactive (LAL) (Benus *et al.* 1991). Using these lines, Veenema

454   *et al.* (2003) showed that response to a chronic stressor resulted in symptoms in LAL

455   (proactive) mice characterized by decreased body weight, elevated plasma adrenocorticotropic

456   hormone (ACTH) and corticosterone levels and a lower hippocampal mineralocorticoid receptor

457   (MR): glucocorticoid receptor (GR) ratio.

458   Korte et al. (2005) mention that adaptive processes, actively maintain stability through change

459   (allostasis) are dependent on the personality type and associated stress responses. The benefits

460   of allostasis and the costs of adaptation (allostatic load) lead to different trade-off in health and

461   stress related diseases, reinforcing that both coping styles (proactive/reactive) can be successful,

462   under different environmental conditions.

463   Furthermore, van de Nieuwegiessen *et al.* (2010) showed that chronic stressors (stocking

464   density) affect the performance traits in African catfish differently according to coping

465   strategies. Fish housed at high density showed an increase in activity and decrease in aggression

466   levels. In addition, at high density, reactive individuals reared in mixed groups showed a

467   comparable growth rate to intermediate and proactive individuals. It seems that the presence of

468   intermediate and proactive individuals stimulates the feeding motivation of reactive individuals.

469   Undoubtedly, coping styles play an important role in how different individuals appraise the

470   housing environment and thereby their welfare status. Huntingford & Adams (2005) reviewed

471   the welfare consequences of coping strategies in Salmonids. They suggest that when fish are

472   housed at high densities and with a predictable feed source, as is usually the case in intensive

473   husbandry systems, reactive individuals may fail to flourish. Another interesting question

474   related with high densities, is the difference on how proactive and reactive individuals react to

475   the suppression of aggressive behaviour induced by crowding i.e. the propensity for higher

476   aggression in proactive individuals suggests that they will suffer most in high densities.

477   In contrast to Huntingford & Adams (2005), no indications were found for welfare

478   consequences of different coping strategies in intensive husbandry systems in African catfish

479   (van de Nieuwegiessen *et al.* 2010). Although an impaired growth performance of reactive fish

480 housed in reactive groups was shown, no effects were detected in reactive fish housed in mixed

481 groups, which is the common rearing practice.

482 Based on these results, individual coping styles should not be used as a welfare indicator, but

483 one may infer a welfare problem when the behaviour identified under the proactive/reactive

484 continuum changes. Even though, the housing environments may have profound effects on

485 behaviour and welfare. For example, in pigs the environmental enrichment effects were shown

486 to be much higher in LR than in HR and were reflected in more time on play behaviour and

487 more oral manipulation of pen mates (Bolhuis *et al.* 2005b). In addition, the same authors

488 showed that the effect of environmental enrichment on weight gain may differ for pigs with

489 divergent coping styles. In fish, the effect of environmental enrichment (i.e. substrate

490 availability) as behavioural and physiological indicators of welfare was study by Galhardo *et al.*

491 (2008) whom showed that the absence of substrate decreased territorial behaviour, increase

492 aggression levels, cortisol and glucose; all of which are suggestive of a stress-related context.

493 This suggests that the welfare of at least some fish species may be negatively affected by the

494 absence of substrate or other environmental enrichment, and this effect may change in distinct

495 fish coping styles.

496 Furthermore, aggressiveness level is one of the differences between proactive and reactive

497 individuals. Literature suggests that proactive individuals show high levels of aggressiveness

498 (Øverli *et al.*, 2004 Castanheira *et al.*, 2013b). Aggression has been linked with a diversity of

499 aquaculture-relevant problems including decreased feed intake, growth dispersion, chronic

500 stress and disease vulnerability (Huntingford & Adams 2005; Martins *et al.* 2011e) which as a

501 consequence can impair fish welfare.

502 Moreover, Vindas *et al.* (2012, 2014) showed good evidence that Atlantic salmon possess a

503 nervous system and a brain sufficiently complex to demonstrate individual responses to

504 frustrations conditions when an omission of an expected reward occurs. Deviation from routine

505 feeding practices, in intensive farming conditions, could have negative consequences, in terms

506 of both production and welfare as a consequence of frustration-induced agonistic behaviours.

507 Knowing that farmed fish have coping styles and that coping styles differ in how they appraise

508 their environment may help designing farming environments that are more diverse and could

509 improve the welfare of individuals with different coping styles. In turn, this may increase

510 production output.

511 *Flesh quality*

512 Nowadays there is evidence showing that inadequate fish husbandry results in lower meat

513 quality (Ribas *et al.* 2007; Robb *et al.* 2000; Matos et al., 2010, 2011). Studies show that fish

514 subjected to stress prior to and during slaughter, in particular salmonids, display a softer texture

515 and lower flesh quality (Bahuaud *et al.* 2010; Kiessling *et al.* 2004). Some studies suggest that

516 the production of low cortisol-responsive fish could benefit commercial parameters such as

517 flesh quality (Pottinger 2001). High fillet quality (e.g. textural characteristics, freshness and

518 health value) is a requirement for feed production and coping styles can attenuate or aggravate

519 the effect of stressors on filet quality. However, knowledge on the mechanisms responsible for

520 individual differences in flesh quality is still largely unknown.

521

522 *Production systems*

523 It is also important to understand how divergent coping styles perform in different aquaculture

524 production systems. Recirculating Aquaculture Systems (RAS), for example are expected to

525 expand in the future as they offer the possibility to have a high production with a minimum

526 ecological impact (Martins et al. 2010).

527 Mota *et al.* (2014) showed that steroids (glucocorticoids, androgens and a progestin) in their

528 free and conjugated forms tend to accumulate in the rearing water of commercial RAS at levels

529 that can potentially be detected by some fish species. However, we still do not know how

530 sensitive the different coping styles are to the re-uptake of steroids and olfactory cues present in

531 the water and how such sensitivity can induce different welfare levels.

532 Furthermore, the range of the coping styled spectrum that leads to maximum growth

533 performance, highest welfare condition and disease resistance, may change depending on the

534   husbandry system, once different types of intensive, semi-intensive or extensive systems present

535   very different social and environmental conditions to fish.

536   **Future perspectives**

537   Coping styles are present in a variety of farmed fish and may impact aquaculture in different

538   ways. However, one of the main difficulties in understanding the implications of coping styles

539   under farming conditions is the methodology available that relies heavily on individually-based

540   tests. Screening in isolation may induce significant stress in social species. Consequently, the

541   development of grouped-based tests (Figure 2) may in the future facilitate mass screening of

542   fish stocked at high densities and therefore may be more easily applied under farming

543   conditions. Examples of potential mass screening tests are the hypoxia and the risk-taking tests

544   (Millot *et al* 2009b; Huntingford *et al.* 2010; Laursen *et al.* 2011; Castanheira *et al.* 2013b).

545   Additionally, further studies should be considered to validate the temporal consistency over

546   time of the distinct traits. One of the limitations of the available knowledge regarding the

547   temporal consistency is that it refers always to short term consistency (usually a few weeks)

548   (Basic *et al.* 2012; Castanheira *et al.* 2013b). However, van Reenen (2012) demonstrated long-

549   term consistency of individual differences in behavioural and adrenocortical responses of dairy

550   cattle to acute stressors. The observations were recorded in rearing period (6 - 7 months),

551   gestation (22 - 24 months) and first lactation (25 - 29 months). They showed that individual

552   differences in struggling in a restraint test at 7 months of age predicted those in open field

553   locomotion during first pregnancy. In addition, individuals with high cortisol responses and

554   reactive behaviour measured as high avoidance and less exploration to open field and novel

555   object tests at 6 months of age, also exhibited high cortisol responses to both tests at 29 months

556   of age. Similar studies, over longer periods of time should be undertaken also in fish.

557   Measures of HPA axis reactivity, locomotion, vocalisation and adrenocortical and behavioural

558   responses to novelty contributed to the understanding of ability to cope with stress and

559   supporting the idea that stress responsiveness may be mediated by multiple independent

560   underlying traits. Some authors have suggested that cortisol and behavioural responses to

561   stressors are linked to two independent dimensions of stable trait characteristics (Koolhaas *et al.*

562   2010). These authors suggested that the quality of the response to a challenging condition

563   (coping style) is independent from the quantity of that response (stress reactivity). According to

564   the same authors, the physiological responses to stress such as the HPI axis reactivity (one of

565   the most significant differences between proactive and reactive individuals) is more related to

566   an emotional response to stress than to coping styles. Eventually a decoupling of these axis,

567   coping styles and emotional, could bring new light to understand the pronounced individual

568   variation in plasma cortisol response observed. It is also important to perform studies regarding

569   the influence of age, environmental conditions, nutrition and social group in coping styles. In

570   other comparative models (e.g. cows, pigs) coping styles can change partly according to the

571   social environment (van Reenen 2012; van Erp-van der Kooij *et al.* 2003). In addition, van Erp-

572   van der Kooij *et al.* (2003) showed that coping styles in piglets can change according to the

573   social environment although at an older age, this ability was lost.

574   In addition, different coping styles also differ in their adaptability towards shifts in

575   environmental conditions. In mice Benus *et al*. (1988) showed that individual differences in

576   aggressiveness (a component trait of coping styles) explain differences in adaptation to external

577   factors. The adaptation to a new photoperiod cycle took two fold long in the aggressive mice.

578   However, in farmed fish there are no similar studies in literature.

579   Still, studies in farmed fish such as the selected trout lines can open the possibility to use fish as

580   simpler models to understand underlying mechanism of coping styles in vertebrates such as

581   those related to neural activity and their implications in behaviour.

582   The knowledge of coping styles can help to improve the sustainability of production through the

583   establishment of more fine-tuned culture strategies. In this way the feed waste can be minimized

584   since each coping style is related to particular physiological and behavioural responses and

585   some culture variables could be adjusted. Moreover, the genetic basis (heritability/epigenetics)

586   of coping styles, disease susceptibility as well the neuroendocrine mechanisms behind

587   consistent as well as flexible behavioural patterns are here pinpointed as central themes and

588   open research lines on application of coping styles to aquaculture.

589 **Conclusions**

590 The presence of coping styles is now well recognised in farmed fish and its implication for

591 aquaculture can be wide as here reviewed. Taken together, the fairly extensive literature on

592 coping styles in fish shows that screening for coping styles is species-specific. The recent

593 development of group-based tests and the use of proxies may provide an opportunity for mass

594 screening in the future. Mass screening into different coping styles may help optimizing the

595 production systems as optimal conditions for proactive individuals are likely to be different

596 from those of reactive individuals.

597 In addition, the recognition that farmed fish exhibit coping styles means that a number of

598 behavioural and physiological responses will vary as part of a common ―pakage‖ that should

599 be taken into consideration when designing selection programs.

600

606

607

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Figure 1. Distinct pigmentation profiles in Atlantic salmon defined as A) 'spotted', i.e. stress resistant and proactive and B) 'non-spotted', i.e. stress sensitive and reactive. Reproduced with permission from Kittilsen *et al*. 2009

Figure 2. Schematic representation of the group based tests used to determine coping styles in Gilthead seabream *Sparus aurata*. Reproduced with permission from Castanheira *et al*. 2013
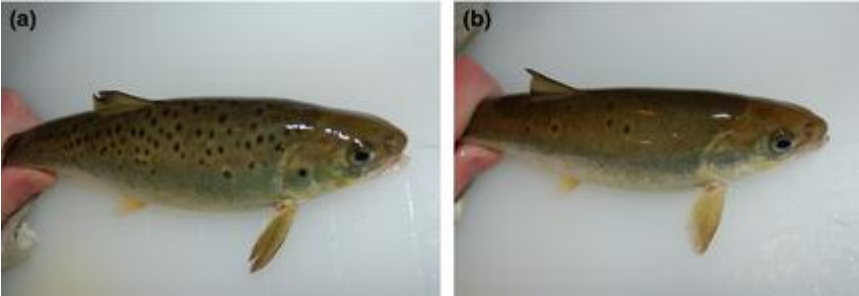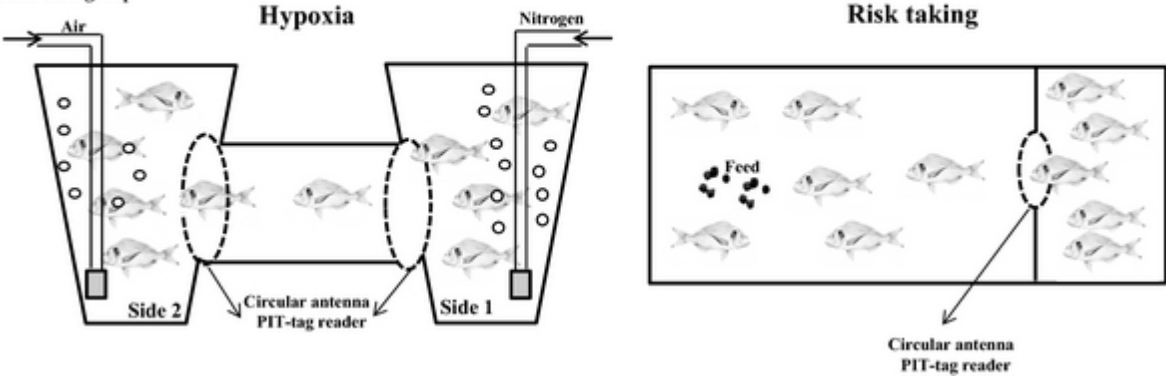
Figure 1

Figure 2

Table.1 Summary of the terminology used concerning individual variation

Individual variation and Terminology

	Terminology	Definition	References
Consistency in behaviour	**Personality (temperament)**	Those characteristics of individuals that describe and account for consistent patterns in feeling, thinking and behaving.	Francis 1990 Gosling 2001
Correlation between behaviours	**Behavioural syndromes**	A suite of correlated behaviours reflecting individual consistency in behaviour across multiple situations	Shi *et al.* 2004
Correlation between behaviour and physiology	**Stress coping styles**	A coherent set of behavioural and physiological stress responses which is consistent over time and which is characteristic of a certain group of individuals	Koolhaas *et al.* 1999

Table.2 Behavioural and physiological differences between proactive and reactive fish

Behavioural characteristics

	Proactive	Reactive	References
Actively escape to stressor	High	Low	Silva *et al.* 2010; Martins *et al.* 2011c; Brelin *et al.* 2005; Laursen *et al.* 2011
Feed efficiency	High	Low	Martins *et al.* 2005ab 2006ab; van de Nieuwegiessen *et al.* 2008
Feeding motivation	High	Low	Øverli *et al.* 2007; Kristiansen & Fernö, 2007
Risk taking and exploration	High	Low	Huntingford *et al.* 2010; Øverli *et al.* 2006; MacKenzie *et al.* 2009; Millot *et al.* 2009a
Aggressiveness	High	Low	Øverli *et al.* 2004, 2005; Castanheira *et al.* 2013
Social influence	Low	High	Magnhagen, 2007; Magnhagen & Staffan 2005; Magnhagen & Bunnefeld, 2009
Sensitive to environmental stressors	Low	High	Höglund *et al.* 2008
Plasticity/Flexibility/Routine formation	Low	High	Chapman *et al.* 2010; Ruiz-Gomez *et al.* 2011

Physiological characteristics

	Proactive	Reactive	References
HPI reactivity	Low	High	Castanheira *et al.* 2013a; Øverli *et al.* 2006; Trenzado *et al.* 2003
Sympathetic reactivity	High	Low	Schjolden et al. 2006; Verbeek et al. 2008; Barreto & Volpato 2011
Parasympathetic reactivity	Low	High	Verbeek et al. 2008 Barreto & Volpato 2011
Hormonal modulation	Low	High	LeBlanc *et al.* 2012
Oxygen consumption	High	Low	Herrera *et al.* 2014; Killen *et al.* 2011, Martins *et al.* 2011c
Myocardial dysfunction	Low	High	Johansen *et al.* 2011
Neural plasticity	Low	High	Johansen *et al.* 2012
Immunity	High	Low	Kittilsen *et al.* 2012

Table 3 A. Summary of the evidence of coping styles in farmed fish and common tests used-
Freshwater Fish

Freshwater Fish				
Fish Species	**Tests**	**Screening**	**Observations**	**References**
Common carp (*Cyprinus carpio*)	Risk-taking, competitive ability	Group	Rate of exploration and competitive ability are consistent over time and related to risk-taking behaviour: individuals that explored more quickly the novel environment were the first to gain access to restricted feed.	Huntingford *et al.* (2010)
	Risk-taking	Group	Individual differences in behavioural responses, immune condition and baseline gene expression.	MacKenzie *et al.* (2009)
Nile tilapia (*Oreochromis niloticus)*	Feed intake recovery	Individual	Individual differences in ventilation rate and correlate with the rate of feeding recovery in isolation.	Barreto & Volpato, 2011
	Feed intake recovery	Individual	Proactive individuals seem to exhibit a faster recovery of feed intake after transfer into a novel environment and use feed resources more efficiently.	Martins *et al.* (2011 bd)
	Feed intake recovery, novel object, restraining	Individual	Inclusion of emotional reactivity (fearfulness) and appraisal as discriminating variables between reactive and proactive individuals.	Martins *et al.* (2011a)
African catfish (*Clarias gariepinus)*	Feed intake recovery, feeding behaviour	Individual + Group	Proactive individuals seem to exhibit a faster recovery of feed intake after transfer into a novel environment and use feed resources more efficiently. Feeding behaviour could be used as a predictor of feed efficiency.	Martins *et al.* (2005ab; 2006 abc)
	Feed intake, aggression	Individual + Pairwise	Individual differences in residual feed intake are related with differences in aggressive behaviour: more efficient individuals are more aggressive.	Martins *et al.* (2008)
	Alarm cues, feeding behaviour	Individual	Feeding efficiency (residual feed intake) related with opposite behavioural responses to conspecific skin extract.	van de Nieuwegiessen *et al.* (2008)
	Escape test	Individual + Group	Behavioural responses to the escape test (after a group-housed period) changed according to the group composition.	van de Nieuwegiessen *et al.* (2010)
Perch (*Perca fluviatilis*)	Habitat utilisation and feeding activity in visual contact with a potential predator, Risk-taking	Individual + Group	Proactive individuals spent more time in the open field and tended to be faster to enter in unknown environments. Modulation of individual behaviours by other group members.	Magnhagen & Staffan (2005) Magnhagen (2007) Magnhagen &Bunnefeld (2009)

Table 3 B. Summary of the evidence of coping styles in farmed fish and common tests used-
Diadromous Fish

Diadromous Fish				
Atlantic salmon (*Salmo salar*)	High/Low stress response	-	Individual differences in disease resistance in lines selected for high and low post stress plasma cortisol levels.	Fevolden *et al.* (1993)
	Feeding in isolation, confinement	Individual	HR (more reactive) fish showed increased susceptibility to infectious. Pigmentation profiles are correlated with stress cortisol response. Distinct vulnerability to parasites correlates with pigmentation (high/low black skin spots).	Kittilsen *et al.* (2009;2012)
	Resume feeding in isolation	Individual	Early emerging individuals showed a shorter time to resume feeding after transfer to rearing in isolation.	Vaz-Serrano *et al.* (2011)
Rainbow trout (*Oncorhynchus mykiss*)	Aggression	Pairwise	Lower brain serotonergic activity in socially naïve fry with big yolk and higher propensity for social dominance and aggression.	Andersson & Höglund (2012)
	Emergence from spawning gravel	Group	Relationship between characteristics expressed in early development and stress coping styles. The LR fish line has bigger eggs, yolk reserves and faster developmental rate.	Andersson *et al.* (2013a,b)
	Novel object , resident intruder, confinement	Individual	Individual differences were behavioural constant, but no differences were found between LR-HR lines.	Basic *et al.* (2012)
	Confinement	Group	Inflammatory challenge with bacterial pathogens reported distinct disease resistance between coping styles.	Fevolden *et al.* (1992)
	Novel object	Individual	Social context is an important modulator of coping styles. Bold fish may be more flexible to changing conditions as opposed to shy individuals.	Frost *et al.* (2007)
	Initiation of avoidance swimming (larvae)	Individual	Yolk-sac fry originating from the HR strain were more sensitive to environmental stressors, and have shown a shorter reaction time to low oxygen levels.	Höglund *et al.* (2008)
	Confinement	Individual	HR fish seem to be associated with cardiac remodeling and altered gene expression.	Johansen *et al.* (2011)
	Confinement, social stress (dominant resident fish)	Individual + Group	Neurobiological mechanism underpinning differences in plasticity associated with distinct coping styles.	Johansen *et al.* (2012)
	Confinement	Individual	Differences between the HR-LR fish strain in the degree of pigmentation.	Kittilsen *et al.* (2009b)
	Hypoxia	Group	Behavioural responses to hypoxia can be used as a non-invasive method for sorting fish according to stress coping styles.	Laursen *et al.* (2011)
	Confinement, heat shock, feed intake recovery	Individual	HR fish has a general response to environmental changes reflected in their greater and faster heat shock response and lower oxidative protein damage in response to high temperatures.	LeBlanc *et al.* (2012)

	Exploratory behaviour, Risk-taking	Individual + Group	The importance of the genetic regulation: isogenic lines with contrasted behavioural responses to a set of environmental stimuli.	Millot *et al.* (2014b)
	Emersion, confinement	Group	HR-LR individuals differed in memory retention.	Moreira *et al.* (2004)
	Locomotor activity, smaller conspecific intruder, feed intake	Individual + Pairwise	Behavioural and physiological differences between HR and LR fish established differences in performance.	Øverli *et al.* (2002)
	Aggressive behaviour , feed intake, confinement	Individual + Pairwise	LR fish were more aggressive when placed in a dominant social position.	Øverli *et al.* (2004a)
	Confinement, locomotor activity, feed intake	Individual	Individual differences in behavioural responses. Synthesis and metabolism of monoamine neurotransmitters and their metabolites were elevated after stress to a larger degree in HR fish.	Øverli *et al.* (2004b)
	Feed intake recovery, confinement	Individual	Behavioural indicators of stress-coping styles related with sex difference. Immature males resumed feeding after transfer to social isolation quicker than males. Females settling down and ceasing to move in a panic-like manner quicker than males during the confinement.	Øverli et al. (2006a)
	Crowded/ uncrowded conditions	Group	Distinct susceptibility under crowded condition and more feed waste in units containing HR when transported.	Øverli *et al.* (2006b)
	Feeding behaviour	Individual	Differences in responsiveness to environmental change: LR fish shown to develop routines more easily.	Ruiz-Gomez *et al.* (2011)
	Feed intake recovery, conspecific intruder	Individual + Pairwise	Behavioural plasticity is limited by genetic factors determining social position in early life. Some behavioural differences can be modified by experience.	Ruiz-Gomez *et al.* (2008)
	Confinement	Group	Differences between the HR-LR fish in plasma amino acids and liver glycogen concentration.	Trenzado *et al.* (2003)
	Crowded/ uncrowded conditions	Group	Performance discrepancy between the HR-LR fish related with competitiveness/ aggressiveness. Differences in plasma glucose levels and glycogen levels.	Trenzado *et al.* (2006)
Brown Trout (*Salmo trutta*)	Feed intake recovery, resident-intruder, hypoxia, confinement	Individual	Individual differences in behavioural responses on resident-intruder, hypoxia and confinement. No differences in feed intake recovery.	Brelin *et al.* (2005)

Table 3 C. Summary of the evidence of coping styles in farmed fish and common tests used-
Marine Fish

Marine Fish				
Gilthead Sea bream (*Sparus aurata*)	Restraining, aggression	Individual + Pairwise	Fish with lower cortisol levels (proactive) when exposed to stress are more aggressive.	Castanheira *et al.* (2013b)
	Feed intake recovery, novel object, restraining, risk-taking	Individual + Group	Behavioural differences are consistent over time and predictable based on other behaviours. Possibility to predict behaviour in groups from individual personality traits.	Castanheira *et al.* (2013a)
	Risk-taking, hypoxia	Individual + Group	Risk-avoiders (reactive) behaviours were negatively correlated to movement and oxygen consumption rates in metabolic chambers.	Herrera *et al.* (2014)
Sea bass (*Dicentrarchus labrax*)	Feed intake recovery, exploration, restraining, risk-taking, hypoxia	Individual + Group	Behavioural differences were not consistent over time or across context in individual-based tests. In contrast, strong individual consistency was observed for all variables measured in group based tests. Hypoxia-avoiders had lower cortisol rate, higher activity and were higher risk-takers: the 3 characteristics of proactive coping style	Ferrari *et al.* (2014)
	Exploration + swimming activities after a stimulation	Individual	Whatever the level of domestication and selection for growth fish presented the same flight response and stimulus exposure induced a significant decrease in exploratory behaviour and swimming activity. Only one generation of captivity could be sufficient to obtain fish presenting the same coping style characteristics (bolder) than fish reared for at least two generations.	Millot *et al.* (2009a)
	Risk-taking	Group	Wild fish were generally bolder than selected fish during two first days of test but showed a decrease in risk taking behaviour during a third day test. Selected fish showed a constant increase in their risk-taking behaviour over time.	Millot *et al.* (2009b)
Senegalese sole (*Solea senegalensis*)	Feed intake recovery, restraining	Individual	Proactive fish exhibit shorter feeding latency, higher duration of escape attempts and lower undisturbed cortisol levels than passive individuals.	Silva *et al.* (2010)
	Restraining	Individual	Individual differences in metabolism are predictive of distinct coping styles.	Martins *et al.* (2011a)
Sole (*Solea solea*)	Novel environment, light avoidance, feeding efficiency	Group + Individual	Proactive fish (high swimming activity) were most feed efficient and grew faster.	Mas-Muñoz *et al.* (2011)
Halibut (*Hippoglossus hippoglossus*)	Swimming behaviour, feed intake	Group	Reactive individuals were unable to adapt, or adapted very slowly, to floating feed showed decreased feed intake and increased stereotypic (surface swimming) activity – reflects high routine formation.	Kristiansen & Fernö (2007)