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1 **Fish facing global change: are early stages the lifeline?**

2  
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4  
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10  
11 **Abstract**

12  
13 The role of phenotypic plasticity in the acclimation and adaptive potential of an organism to  
14 global change is not currently accounted for in prediction models. The high plasticity of marine  
15 fishes is mainly attributed to their early stages, during which morphological, structural and  
16 behavioural functions are particularly sensitive to environmental constraints. This  
17 developmental plasticity can determine later physiological performances and fitness, and may  
18 further affect population dynamics and ecosystem functioning. This review asks the essential  
19 question of what role early stages play in the ability of fish to later cope with the effects of  
20 global change, considering three key environmental factors (temperature, hypoxia and  
21 acidification). After having identified the carry-over effects of early exposure reported in the  
22 literature, we propose areas that we believe warrant the most urgent attention for further  
23 research to better understand the role of developmental plasticity in the responses of marine  
24 organisms to global change.

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25 *Key words:* early environmental history, developmental plasticity, marine fishes, temperature,  
26 hypoxia, acidification.

27

## 28 **Highlights**

29

- 30 • The potential benefits of plasticity depend on several factors
- 31 • Further knowledge of concurrent effects of several environmental factors is needed
- 32 • It is also crucial to pursue and deepen transgenerational work
- 33 • Models should take phenotypic plasticity into greater account

34

## 35 **1. Introduction**

36

37 A major current scientific challenge is to understand and predict responses of marine  
38 ecosystems to global change in order to preserve biodiversity and ecosystem services on which  
39 human life depends (Chapin et al., 2000). This challenge implies a better understanding of the  
40 functional processes of these systems at different scales of organisation (i.e., trophic web,  
41 species, populations, organisms, tissues, cells, molecules) and time (i.e., life cycle, day, seasons,  
42 year, etc.) in response to environmental variability. The overall goal is to develop robust tools  
43 that inform stakeholders and policy-makers, enabling them to make environmental policy  
44 decisions. It is therefore necessary 1) to gain knowledge on the capacity of marine animals to  
45 cope with changing environments and 2) to incorporate proximal biological mechanisms of  
46 acclimation and adaptive response (microevolution and phenotypic plasticity) in predictive  
47 models linking climate scenarios to species distribution and abundance.

48 Faced with environmental variability, a species may respond by (1) a shift of its  
49 distribution, (2) an acclimation when exposed to intermittent and rapid changes, or (3) an

50 adaptation, which implies genetic selection over generations (Hoffmann and Sgrò, 2011;  
51 Munday et al., 2013).

52         Acclimation and adaptive capacity to a changing environment are forms of  
53 environmental responsiveness resulting from phenotypic plasticity (Lande, 2009), which is  
54 defined as the ability of an organism to respond to an environmental input with a change in  
55 form, state, movement or rate of activity (West-Eberhard, 2005). Phenotypic plasticity is the  
56 ability of a single genotype to produce more than one alternative phenotype in response to  
57 environmental conditions (Relyea and Hoverman, 2003; Robinson and Parsons, 2002;  
58 Schlichting and Pigliucci, 1998; West-Eberhard, 1989). Plasticity can be characterized at  
59 different levels of organization from the molecular to the social. It can be continuous or  
60 discontinuous, reversible or irreversible, and adaptive, maladaptive or neutral with regard to an  
61 individual's fitness (Hendry, 2016; Schlichting and Pigliucci, 1998). The degree to which  
62 plasticity is adaptive or maladaptive depends on whether environmentally-induced phenotypes  
63 are closer or further away from the new optimum (Ghalambor et al., 2007; Lande, 2009;  
64 Schlichting and Pigliucci, 1998). The concept of parsimony of selection would suggest that  
65 plasticity should be adaptive in inducing one or several alternative phenotypes representing  
66 fitness-optimizing strategies in response to a specific environmental challenge. However,  
67 adaptive plasticity is likely to be the product of past selection on variation that may have been  
68 initially maladaptive (Ghalambor et al., 2015, 2007). So, it is difficult to establish a conceptual  
69 framework to predict the role of plasticity, whether adaptive or maladaptive, in response to  
70 global change.

71         The time of maximal plasticity in the life of an organism appears to be during its  
72 development. Plasticity in developmental programming, or developmental plasticity (DP), has  
73 evolved in order to give organisms in changing environments the best chances of survival and  
74 reproductive success (Bateson et al., 2014; Gilbert, 2001; West-Eberhard, 2005). The concept

75 of developmental plasticity therefore implies a controlled process of disruption by the  
76 environment of the developmental programme operated by inherited genes in early stages (egg,  
77 embryo, larvae), rather than random variations or “noise” in their developmental programme.  
78 The effects of a changing environment occurring during these early stages can sometimes be  
79 observed later on, so the environment experienced during early stages can affect the juvenile or  
80 adult phenotypes through carry-over effect, programming, or conditioning (Burton and  
81 Metcalfe, 2014; Jonsson and Jonsson, 2014; Pankhurst and Munday, 2011). The role of this  
82 developmental plasticity in the acclimation and adaptability of organisms in the face of global  
83 change is seldom accounted for in current prediction models (Chevin et al., 2010; Frieler et al.,  
84 2012; Nettle and Bateson, 2015). Current models usually consider rapid environmental changes  
85 without taking into account the adaptive potential of a species (Doney et al., 2012; Poloczanska  
86 et al., 2013; Veron, 2008; Harley et al., 2006).

87         Developmental plasticity occurs within one generation, and in this sense, the concept  
88 differs from transgenerational plasticity (TGP), which occurs when the phenotype of a new  
89 generation is influenced by the environment experienced by the previous generation(s)  
90 (Donelson et al., 2017). TGP is a non-genetically inherited phenotypic response where the  
91 environment experienced by the parents influences offspring reaction norms (i.e., the particular  
92 way a phenotype varies across environments, Woltereck, 1909), resulting in different  
93 phenotypes expressed by the same genotype in different environments (Bonduriansky et al.,  
94 2012; Salinas et al., 2013; Shama and Wegner, 2014).

95         The mechanisms underlying phenotypically plastic impacts, within or across  
96 generations, are not well known and are still a matter of discussion (Torda et al., 2017). It has  
97 been hypothesized that epigenetic changes, namely DNA methylation and histone  
98 modifications, would be one of these mechanisms. Epigenetic regulations are induced by the  
99 environment and occur without any changes to the DNA sequence, but for example influence

100 chromatin structure, then alter access of transcriptional factors to DNA and ultimately modify  
101 gene expression sequences (Le Roy et al., 2017). Such epigenetic modifications can be inherited  
102 within chromosomes (Beldade et al., 2011; Campos et al., 2014; Goldberg et al., 2007), and it  
103 has been hypothesized that, if the environment remains relatively stable for the time required  
104 for several generations, their effects will occur gradually over several generations instead of  
105 taking place all at once (Burggren, 2015). It has been shown in mammals that these induced  
106 phenotypic changes can sometimes persist long after the environmental stress ceased, offering  
107 a potential target for natural selection (Turner, 2009).

108         Among marine organisms, fish constitute a highly plastic group with a great ability to  
109 modify their phenotype in relation to environmental conditions, especially during their early  
110 ontogenetic period when substantial changes in structure, physiology and morphology occur.  
111 This developmental plasticity has been shown to have long lasting consequences by  
112 determining later physiological performance in terms of survival, growth, swimming  
113 performance, predator avoidance, size at ontogenetic niche shifts, age at maturity, fecundity,  
114 egg size and lifespan (Jonsson and Jonsson, 2014). This consequently impacts the functional  
115 capabilities of fish to cope with a changing environment in terms of recruitment, migration or  
116 predation, for example. In addition to providing multiple ecosystem services, fish constitute a  
117 crucial compartment within the marine food web (from primary consumers to top predators).  
118 The modification of their physiological performances, in terms of locomotion or predation rate  
119 for example, may affect energy and matter fluxes between the compartments of the food web  
120 and have consequences for the functioning of the whole ecosystem. This developmental  
121 plasticity and its long-term effects are commonly used in aquaculture systems to control  
122 phenotypic characteristics of high importance for the quality of commercial fish, such as sex  
123 ratio (Navarro-Martín et al., 2009), body shape, growth, or flesh omega-3 content (Tocher,  
124 2015; Vagner et al., 2009, 2007).

125           In this review, we ask what the roles of developmental and transgenerational plasticity  
126 could be in inducing plastic responses in fish that favour later-life acclimation to global change.  
127 We also ask about the possible involvement of selection when response variations are heritable  
128 and influence fitness. These questions are of key ecological importance because such processes  
129 can drive evolution (Robinson, 2013). They are also of economic importance because of the  
130 central role of fish within the marine trophic web, and because they provide a large portion  
131 (20%) of the human demand for protein and omega-3 fatty acids (Food and agriculture  
132 organization of the United States., 2014). Moreover, fish are particularly exposed to global  
133 change as, many species depend on coastal zones to complete their life cycles and these areas  
134 are particularly exposed to environmental variability.

135           The aim of the present work is to review how the early environmental history of fish  
136 can guide the physiological functions of later stages in their ability to cope with changes in key  
137 environmental factors resulting from global change. When possible, this review will consider  
138 the physiological pathways involved, the main chains of events, and the strongest drivers  
139 underlying fish response to an environmental signal experienced during the early stages of life.  
140 This review will analyse the role of developmental and transgenerational plasticity in  
141 facilitating adaptive evolution of natural fish populations to global change. It will focus on  
142 water temperature, ocean acidification and hypoxia, the three key environmental factors that  
143 (1) are changing as a consequence of climate change and (2) have been defined as determining  
144 factors for the maintenance of physiological functions in fish (Fry, 1971; Pörtner, 2005). It will  
145 also consider the combination of these factors, whose effects have only been examined together  
146 in a few studies. Though this examination of past research, this review aims to highlight existing  
147 gaps in the literature on phenotypic plasticity in marine fishes exposed to global change,  
148 providing several possible directions for further research. Through its analysis, this review also

149 emphasizes the necessity to account for phenotypic plasticity within models predicting the  
150 responses of ecosystems to global change.

151

## 152 **2. Methodology used to select the articles that have been included**

153

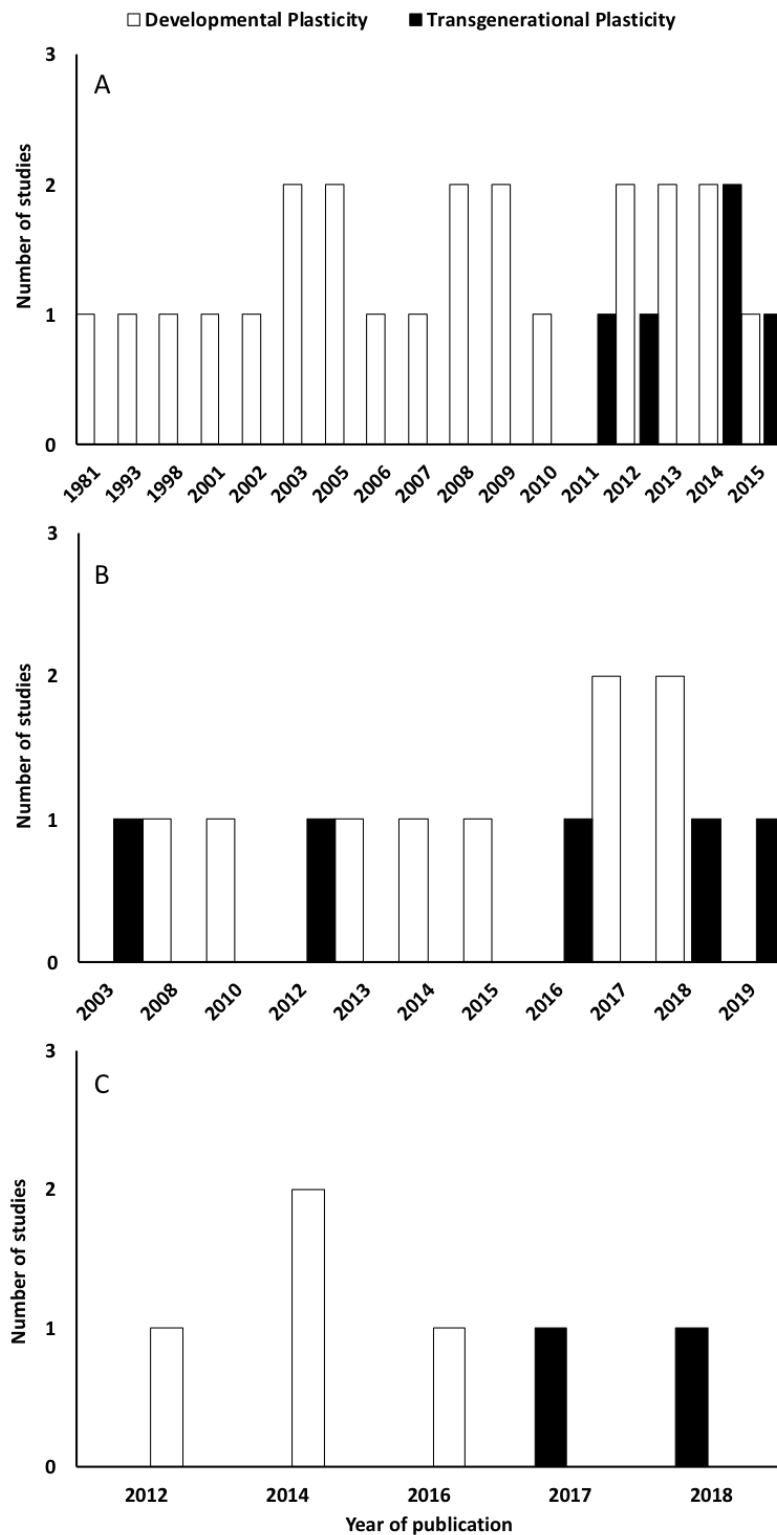
154 Papers included in this review have been selected in databases (Google Scholar, Scopus,  
155 Science direct, Pubmed) using key words such as “plasticity”, “phenotypic plasticity”,  
156 “transgenerational plasticity”, “developmental plasticity”, “early life stage”, “early life  
157 history”, “environmental history”, “long term effects”, “carry over effects”, associated with  
158 “fish”, “marine fish”, “marine teleosts”, as well as with “environmental parameters”,  
159 “temperature”, “hypoxia”, “acidification”, “global change”, “climate change”.

160 No limit of date was applied, and the date of the oldest publications related to each  
161 environmental factor is indicated in the figure legends. Most of the articles concerning the long  
162 term effect of early conditioning to one or to a combination of the environmental factor(s)  
163 considered were selected for this review. Even if they did not specifically tested future  
164 environmental conditions expected with global change, they were considered as papers of  
165 interest to evaluate the fish ability to cope with environmental variability.

166 With this method, a total of 49 papers has been selected for this review. Among them, 28  
167 concerned the effect of temperature (publication period from 1981 to 2015), 14 concerned  
168 hypoxia (publication period from 2003 to 2019), and 6 concerned acidification (publication  
169 period from 2012 to 2018). Only one article concerned the combined effects of these three  
170 factors on later life stages, and it was published in 2013. The Fig. 1 presents the distribution of  
171 48 out of the 49 articles selected (the one reporting the effects of combined factors is not  
172 included in the figure) across time, environmental factor, and type of plasticity (development  
173 or transgenerational plasticity).

174





175  
176  
177

178 **Fig. 1.** Distribution of the papers included in the present review across time, environmental  
179 factors (A: temperature; B: hypoxia, C: acidification), and type of plasticity (white and black  
180 bars respectively represent developmental plasticity and transgenerational plasticity).

181

### 182 **3. Temperature**

183

184 Among the environmental factors influenced by global change, temperature is, by far, the most  
185 documented as concerns effects on developmental plasticity. The atmosphere and oceans have  
186 warmed unequivocally and rapidly since the 1850s, due to increasing concentrations of  
187 greenhouse gases (IPCC, 2013). Since the 1950s, many of the observed temperature changes  
188 are unprecedented, and the Earth's surface has been successively warmer in each of the last  
189 three decades (IPCC, 2013). The latest reports predict that continued emissions of greenhouse  
190 gases will cause an increase in sea surface temperature ranging from 2 to 4°C throughout global  
191 marine waters by 2100 (IPCC, 2013).

192 Environmental temperature is known to influence the physiology of numerous aquatic  
193 organisms, as most of them, including the great majority of fish species, are poikilothermic.  
194 Such organisms are not able to control their internal temperature, which fluctuates with the  
195 environment (Fry, 1971). Temperature is in fact the most pervasive environmental factor for  
196 these organisms, as it strongly governs their metabolic rates, development, growth, feeding  
197 activity, recruitment, maturity, distribution, and survival throughout the life cycle (Blaxter,  
198 1991; Hochachka and Somero, 2002; Kamler, 1992). These physiological and developmental  
199 processes are optimal within a narrow thermal range, and small changes of external temperature  
200 can alter them in a lasting manner. For several decades, a large number of studies have reported  
201 that a deviation from the optimal developmental temperature range during early life in fish may  
202 cause considerable phenotypic variations at later developmental stages due to the high plasticity  
203 of young stages (Campos et al., 2013; Conover and Kynard, 1981; Georga and  
204 Koumoundouros, 2010; Johnston et al., 2009, 2001; Johnston and Bennett, 2008; Johnston and  
205 Lucking, 1978; Johnston and Temple, 2002; Koumoundouros et al., 2009). By reviewing the

206 effects of early thermal change on later phenotypes, we question the potential role of early life  
207 history temperature as a key factor to determine the ability of fishes exposed to current  
208 environmental thermal changes to cope with their new environment.

209

### 210 *3.1. Effects of early temperature change on larval phenotype*

211

#### 212 *3.1.1. Duration of the larval period*

213

214 The literature includes abundant reports of egg conditioning in a warmer environment leading  
215 to faster larval and juvenile growth that consequently decrease the time spent at each  
216 developmental stage (Grorud-Colvert and Sponaugle, 2011; Martell et al., 2005a, 2005b). For  
217 example, faster growth led to shorter pelagic larval phases in benthic species, such as haddock  
218 *Melanogrammus aeglefinus* and bluehead wrasse *Thalassoma bifasciatum*, whose eggs were  
219 incubated in warmer waters (Martell et al., 2005a). As the larval stage is a period of high  
220 exposure to predation, shortening it could reduce this pressure and lead to a higher survival rate.  
221 Incubation of eggs at warmer temperatures also generally leads to a faster start of the larval  
222 phase in several species (Angilletta and Dunham, 2003; Atkinson and Sibly, 1997; Braun et al.,  
223 2013). In Atlantic salmon *Salmo salar*, this was considered an advantage because it was  
224 associated with longer larvae, and subsequent longer juveniles, leading to higher survival rates  
225 (Braun et al., 2013). In Senegalese sole, a shorter larval phase induced at 21°C was associated  
226 with a higher weight at the pre-metamorphosis stage (Campos et al., 2013).

227

#### 228 *3.1.2. Growth, muscle and swimming performance*

229

230 Incubation temperature can also indirectly affect later growth or survival rates by impacting  
231 energetic metabolism (which affects digestive capacity), or swimming behaviour (which affects  
232 foraging behaviour or predator avoidance). The literature suggests that these effects largely  
233 depend on the magnitude of the warming experienced during early stages. For example, the  
234 incubation of Atlantic herring *Clupea harengus* eggs, which usually experiment high  
235 temperature variability in natural environment (from about 5 to 14°C), at 12°C led to enhanced  
236 swimming capacities in later larvae in terms of higher maximum velocities during fast starts  
237 and reduced yaw swimming behaviour compared with larvae that were incubated at 5°C during  
238 egg stage (Johnston et al., 2001). As swimming stamina and initial burst responses are usually  
239 critical swimming characteristics for predator avoidance (Bams, 1967), these results show the  
240 benefit of moderately warmer conditioning of Atlantic herring eggs to improve later escape  
241 performance or prey capture, which indirectly promote growth rate.

242 This enhanced performance could result from an accelerated development, including  
243 flexion of the notochord and development of the dorsal and anal fin ray muscles at shorter body  
244 lengths. It may also be promoted by an increasing cell size and number of myofibrils in  
245 superficial muscle, earlier new myofibril recruitment and larger mean deep muscle size with  
246 warmer temperature (Johnston, 2001). Such effects have been described in Atlantic salmon and  
247 Senegalese sole incubated at higher temperatures during their embryonic stages (8–10°C vs 2–  
248 5°C and 18–21°C vs 15°C, respectively; Campos et al., 2013). Similar effects were noted for  
249 Atlantic cod *Gadus morhua* embryos incubated at 10°C, compared with those incubated at a  
250 lower temperature (Hall & Johnston, 2003; Johnston, 2001; Johnston, 2006).

251 The plastic response of myofibrils to a thermal event occurring early in the life history  
252 has been widely demonstrated in several fish species and appears to result from a modification  
253 of both molecular and cellular processes. Some authors suggested that an increase of 2–3°C in  
254 the water temperature during embryonic development is enough to modify the expression of a

255 subset of transcripts, such as myogenic regulatory factors (MRFs), myosins, igf-1 and fgf6, as  
256 well as the proliferation and differentiation of myogenic progenitor cells and protein synthesis  
257 necessary for skeletal muscle growth (Campos et al., 2013; Johnston, 2006). Muscle plasticity  
258 is usually irreversible during the embryonic and larval stages, due to the rapid pace of  
259 ontogenetic change (Johnston, 2006).

260         Contrary to the beneficial effect of warming (12°C vs 5°C) on swimming performances  
261 observed by Johnston et al. (2001) in Atlantic herring, Batty et al. (1993) reported reduced  
262 larval swimming speed in the same species when eggs were incubated 2°C above the optimal  
263 natural temperature (5°C). These effects could be partly explained by the occurrence of skeletal  
264 deformities induced by incubation at higher than usual/optimal temperatures, as shown in  
265 Senegalese sole (Dionísio et al., 2012). In addition, even a 2°C increase during egg incubation  
266 (14°C vs 12°C) of Sockeye salmon *Oncorhynchus nerka* led to reduced swimming  
267 performances of larvae (Burt et al., 2012). The interval between the initiation of maximum  
268 swimming speed and the time the larvae became tired and stopped swimming was shorter. This  
269 higher rate of fatigue could lead to poor schooling behaviour and decreased survivorship  
270 (Tierney et al., 2009). In a natural environment, changes in swimming ability can have a  
271 profound indirect influence on larval fish growth and survival by modifying foraging success  
272 and predator avoidance capacity.

273

### 274 *3.2. Effects of early temperature change on juvenile phenotype*

275

#### 276 *3.2.1. Muscle growth and swimming performance*

277

278         Carry-over effects of early conditioning in a warmer environment have been mostly  
279 reported as deleterious for the resulting juveniles. For example, Garcia de la serrana et al. (2012)

280 reared different groups of Gilthead sea bream larvae at 17.5–18.5°C and 21–22°C until  
281 metamorphosis and then transferred them to a tank at 21–22°C. They observed persistent effects  
282 of developmental temperature on muscle growth patterns, with 20% less fibres of higher  
283 average diameter in fish acclimated at high temperature than in those of similar body size  
284 acclimated at low temperature. This was sometimes correlated with reduced maximum aerobic  
285 swimming capacities (Garcia de la serrana et al., 2012). In addition, incubations of sea bass  
286 larvae at 20°C *versus* 15°C until metamorphosis produced juveniles with a reduced relative red  
287 muscle area and a decreased number of red myofibres and mitochondria; this was correlated  
288 with reduced maximum aerobic swimming capacities (Koumoundouros et al., 2009),  
289 susceptible to enhance predation (Seebacher and Grigaltchik, 2015).

290

### 291 3.2.2. *Body shape*

292

293 The thermal environment during early stages has also been shown to induce changes in  
294 juvenile body shape (e.g., positions and structures of fins and bones) in European sea bass  
295 (Georgakopoulou et al., 2007) and other species such as seabream (Loizides et al., 2014) and  
296 zebrafish, *Danio rerio* (Georga and Koumoundouros, 2010). Such changes were described for  
297 the first time in different groups of European sea bass juveniles exposed to 15°C and 20°C from  
298 their half-epiboly stage until metamorphosis (Georgakopoulou et al., 2007). Long after the  
299 thermal treatment, fish body shape tended to be thicker in fish incubated at 20°C than at 15°C,  
300 and fin positions significantly affected. Furthermore, the development of median fins was more  
301 advanced in Atlantic herring juveniles incubated at 8°C and 12°C during the embryonic period,  
302 than in those previously incubated at 5°C (Johnston et al., 1998).

303 Several studies suggest that these body shape differences could be a consequence of the  
304 different allometric growth pattern of different organs, tissues and parts of the body. This is

305 known as the metabolic-developmental hypothesis (Fuiman, Poling, & Higgs, 1998; Lindsey,  
306 1988; Murray & Beacham, 1989; Spicer & Burggren, 2003) and is associated with the  
307 differentially affected development or remodelling of muscles and bones (Georga and  
308 Koumoundouros, 2010; Georgakopoulou et al., 2007; Lindsey, 1988).

309 Consequences of such effects of temperature for physiological performance are not  
310 described in these studies but could include effects on swimming capacity, and predator-prey  
311 relationships, thereby influencing fitness.

312

313 In several species, the long-term effect of early life temperature on the development and growth  
314 of juveniles has been partly explained by thermal imprinting on the expression of a number of  
315 genes related to metabolic pathways and influencing growth or development, such as some  
316 micro RNA (miRNA) genes in the pituitary gland, gonads and liver (Bizuayehu et al., 2015;  
317 Garcia de la serrana et al., 2012; Johnston et al., 2009; Jonsson & Jonsson, 2014; Scott &  
318 Johnston, 2012). In Atlantic cod, these effects have been shown to be inducible predominantly  
319 in a time-specific window during development, as different sets of miRNAs were differentially  
320 expressed in juveniles according to the period at which temperature was elevated (i.e. during  
321 embryo incubation or during larval rearing; Bizuayehu et al., 2015).

322

### 323 *3.3. Effects of early temperature change on adult phenotype*

324

#### 325 *3.3.1. Muscles, body shape, and swimming capacity*

326

327 As stated above for the subsequent larval phenotype, the importance of very early life  
328 stages on the ability of adults to cope with a warmer environment appears to depend on the  
329 extent of the warming encountered during the early stages. In Atlantic salmon, a 3°C

330 temperature change during the short window of embryogenesis (from fertilization until the  
331 eyed-stage) dictated the adult myogenic phenotype three years later with significant effects on  
332 the final number, maximum diameter, nuclear density and size distribution of muscle fibres  
333 (Macqueen et al., 2008). The final fibre number was highest for the 5°C treatment and was  
334 reduced for both 2°C and 8°C treatments, showing that the acclimation capacity for this species  
335 lies within a narrow thermal range.

336 Embryonic temperature has also been shown to induce different body shape phenotypes  
337 in terms of fish shape and position of anal, caudal and dorsal fins, as well as gill covers and  
338 lower jaws in adult zebrafish *Danio rerio* incubated at 28–32°C during their pre-hatching period  
339 rather than 22°C (Georga and Koumoundouros, 2010). More recently, Loizides et al. (2014)  
340 revealed a modification of the bases of the supra-occipital and basi-occipital bones of the upper  
341 jaw, as well as of the dorsal, anal and pelvic fins in sea bream reared at 22°C during the  
342 embryonic period, compared with those reared at 16°C and 19°C. All of these modifications  
343 may induce different locomotor behaviour with further impacts on social, migratory, foraging,  
344 or predator avoidance behaviours.

345

### 346 3.3.2. *Sexual differentiation*

347

348 Increase in temperature during a critical stage of development can have an immutable  
349 effect on later adult phenotype through modification of the sex ratio.

350 In many vertebrates, including fish, offspring gender is not immutably determined at  
351 fertilization, but instead can be influenced by environmental physical and social conditions  
352 experienced during a critical stage of development (during embryogenesis or still later); this is  
353 termed environmental sex determination (Angelopoulou et al., 2012; Shine et al., 2002). Among  
354 the physical factors present in natural environment, temperature has been shown to be one of



355 the main factors in environmental sex determination. Even small temperature changes (1–2°C)  
356 occurring at critical developmental stages invariably resulted in highly male-biased sex ratios  
357 (up to 3:1; males:females) in several freshwater and marine species, such as Atlantic silverside  
358 *Menidia menidia* or damselfish (Brown et al., 2014; Conover and Kynard, 1981; Devlin and  
359 Nagahama, 2002; Donelson and Munday, 2015; Navarro-Martín et al., 2009; Ospina-Álvarez  
360 and Piferrer, 2008; Valenzuela et al., 2003). This temperature effect also occurred when parents  
361 were maintained at higher temperatures throughout the breeding season, including  
362 gametogenesis, embryogenesis and hatching periods.

363         The increased number of males with higher temperature could be the consequence of  
364 two possible mechanisms. 1) A high temperature increases growth rate, and fast-growing fish  
365 would differentiate earlier as males than slow growing fish (De Looze and Kraak, 1992). 2)  
366 Higher temperatures inhibit the activity of aromatase, an enzyme producing oestrogens  
367 essential for female sex differentiation in fish (Uchida et al., 2004).

368 A gender bias away from the optimal sex ratio can significantly impact population success  
369 because it reduces effective population size and, consequently, the viability of sensitive stocks  
370 and the number of individuals contributing to reproduction (Donelson and Munday, 2015).  
371 Thus, there is great concern that global warming threatens these populations, as shown in other  
372 ectotherms (Boyle et al., 2014).

373

### 374 *3.4. Effects of early temperature on subsequent progeny – transgenerational acclimation*

375

#### 376 *3.4.1. Sex ratio*

377

378         A recent study demonstrated that gender bias caused by environmental temperature changes  
379 may be overcome in coral reef damselfish depending on the environment previously

380 experienced by their parents or even grandparents, even at a very young stage (Donelson and  
381 Munday, 2015).

382 This transgenerational plasticity was demonstrated by beneficially modified physiological  
383 performances in progenies (compared with their parents) in response to elevated temperature  
384 (Donelson et al., 2011; Donelson and Munday, 2015). When parents were acclimated at 1.5°C  
385 above the temperature usually experienced during early life, the proportion of female progeny  
386 of damselfish was reduced by about 40%, but after only one generation of acclimation to this  
387 warmer environment (+1.5°C), the proportion of female offspring produced was completely  
388 restored for their entire life and remained normal for the next two generations.

389 Nevertheless, when the parents experienced a temperature 3°C above the mean summer  
390 temperature from early life, the proportion of female offspring was reduced by more than 50%  
391 (compared to the control) and remained reduced by 40% after one generation. In addition, fish  
392 that were reared at 3°C above the average summer temperature for two generations did not  
393 produce any offspring at all, due to the direct effect of temperature on the endocrine system  
394 (Donelson & Munday, 2015).

395 These results demonstrate that (1) two generations are enough for this species to adjust their  
396 sex ratio to a new warmer environment if this warming is within a narrow range (+1.5°C); (2)  
397 in this warmer context (+1.5°C) this species seems to adjust its sex ratio in order to insure the  
398 integrity of its reproduction and consequently ensure its survival.

399

#### 400 3.4.2. *Growth and aerobic scope*

401

402 The first evidence of transgenerational plasticity in response to the thermal environment  
403 was found by Salinas and Munch (2012), who showed that sheephead minnow *Cyprinodon*  
404 *variegatus* adaptively program their offspring for maximal growth (Salinas and Munch, 2012).

405 Similarly, in stickleback *Gasterosteus aculeatus*, progeny grew better when they were  
406 conditioned in the same thermal environment as that experienced by their mother (Shama et al.,  
407 2014). However, this beneficial effect was not constant over the growth period, as demonstrated  
408 by the good early growth of the progeny relative to poorer later performance (Shama and  
409 Wegner 2014).

410

411 The benefits of transgenerational plasticity have also been shown in the metabolism (in  
412 terms of aerobic scope) of coral reef damselfish and sticklebacks (Donelson et al., 2011;  
413 Donelson and Munday, 2015; Shama et al., 2014; Shama and Wegner, 2014). Aerobic scope is  
414 defined as the increase in oxygen consumption rate from resting to maximal. It supports  
415 physiological performances in animals such as swimming capacity, growth, or digestion (Brett,  
416 1971; Fry, 1971; Portner and Farrell, 2008). In ectotherms such as fish, aerobic scope is highest  
417 at the optimal temperature but falls when temperature is lower or higher. Coral reef fish parents  
418 that experienced elevated temperatures (+1.5°C and +3°C above the mean summer  
419 temperature) displayed reduced aerobic scope, but when their offspring experienced the same  
420 elevated temperature, they displayed fully restored aerobic scope (Donelson et al., 2011).

421 Epigenetic inheritance may explain the acclimation of aerobic scope within two generations.  
422 Molecular processes that may enable marine fishes to adjust to a warmer future environment  
423 over multiple generations have recently been shown to be dependent on the up-regulation of  
424 genes involved in metabolism, immune and stress response. Heat shock protein genes did not  
425 respond, indicating that they may not be an appropriate indicator of long term acclimation  
426 (Veilleux et al., 2015).

427

428 *3.5. Conclusions*

429

430 This chapter shows that the thermal environment at very early stages plays a crucial role in the  
431 ability of later stages to develop alternate phenotypes through metabolic memory and intense  
432 individual and sub-individual plasticity processes. This developmental phenotypic plasticity  
433 may be adaptive or maladaptive (Fig. 2A, Fig. 3), which seems to depend on the species  
434 considered, the magnitude of the warming, and the critical developmental window at which the  
435 higher temperature is experienced (Table 1).

436 Effects observed on later larvae were beneficial in about half of the studies, while when we  
437 considered later juvenile or adult stages, early life history mainly had unknown or potentially  
438 non-beneficial effects (Table 1). This is also supported by the transgenerational study of Shama  
439 and Wegner (2014) who reported beneficial effects on larval progeny, which became  
440 disadvantageous at a later stage. This strongly underlines the necessity to study the underlying  
441 mechanisms governing developmental and transgenerational plasticity to better understand and  
442 predict such effects of thermal life history on biological mechanisms occurring during  
443 development from larval to adult stages.

444 Several studies indicate that when the temperature experienced at the early stage is about 1.5–  
445 2°C above the temperature usually experienced, physiological performances at later stages tend  
446 to be enhanced (Table 1, Fig. 3), and later progenies are globally able to be resilient, despite  
447 deleterious effects produced in their parents. However, when the temperature experienced  
448 exceeds the temperature usually experienced by more than 3–5°C (Table 1, Fig. 3), more  
449 deleterious effects may appear at later stages, and later progenies seem to be less resilient, or  
450 not resilient at all, even after two generations.

451 One wonders whether progenies acclimated to 1.5°C above their natural current temperature  
452 have acquired new “buffering capacities” that would allow them to cope with additional  
453 warming episodes, leading to potential transgenerational effects and micro-evolution. Such  
454 possibilities could call into question predictive global change scenarios based on present

455 physiological performances. It also highlights the necessity of identifying physiological trade-  
456 offs that could result from these adaptive changes.

457

#### 458 **4. Hypoxia**

459

460 Increasing intensity and frequency of hypoxic events are also direct consequences of  
461 climate change. Global warming, combined with eutrophication, increases the prevalence and  
462 intensity of oxygen (O<sub>2</sub>) depletion in seawater, particularly in coastal and estuarine areas (Diaz  
463 and Rosenberg, 2008; Meire et al., 2013), which serve as nurseries for many fish species. The  
464 conventional definition of hypoxia is when dissolved O<sub>2</sub> is below 2 mg L<sup>-1</sup>, although this level  
465 differs according to the species considered (Vaquer-Sunyer and Duarte, 2008).

466 Oxygen depletion represents an environmental constraint for many marine species since  
467 a high-energy compound (adenosine triphosphate, ATP) required for their anabolism and  
468 cellular processes, is mainly produced by the transfer of electrons from carrying molecules to  
469 molecular O<sub>2</sub> in mitochondria. Hypoxia may thus limit energy production, with consequences  
470 for metabolic, physiological and behavioural functions that are likely to threaten survival or the  
471 fitness of organisms.

472 To cope with low O<sub>2</sub> concentrations, some fish species have developed mechanisms for  
473 ambient O<sub>2</sub> sensing and evolved various physiological and behavioural strategies (Jonz et al.,  
474 2014). These fish can respond to a decrease in ambient O<sub>2</sub> by trying to escape, increasing  
475 ventilation, O<sub>2</sub> extraction and transport, depressing their metabolism (ATP consumption and  
476 demand) or adjusting anaerobic ATP production (glycolysis) to maintain their cellular energy  
477 balance (Bickler and Buck, 2007; Capossela et al., 2012; Mandic et al., 2009). Fish tolerance  
478 of O<sub>2</sub>-depleted environments is based largely on their capacity to withstand metabolic  
479 depression, to mobilize anaerobic metabolic pathways, and to endure ionic and pH disturbances,

480 all of which vary depending on the species, hypoxia intensity, and ontogenetic stage considered  
481 (Bickler and Buck, 2007; Laura Cadiz et al., 2017; Ekau et al., 2010; Hassell et al., 2008;  
482 McKenzie et al., 2008; Pihl et al., 1992; Shang et al., 2006; Shang and Wu, 2004; Weltzien et  
483 al., 1999).

484

#### 485 *4.1. Developmental plasticity at early life stages*

486

487         The high sensitivity and plasticity of early life stages to hypoxia correspond to a wide-  
488 scale gene expression response (Ton et al., 2003). Several studies highlight the impact of  
489 hypoxia on the modulation of genes involved in energy metabolism (oxidative phosphorylation)  
490 and developmental processes (cell proliferation, migration and apoptosis), including key factors  
491 such as hormones involved in sex differentiation and determination (Kajimura et al., 2006; Lo  
492 et al., 2011; Shang et al., 2006; Shang and Wu, 2004; Ton et al., 2003). The Hypoxia Inducible  
493 Factors-1 (HIF-1) pathway could mediate at least a part of these gene regulations (Kajimura et  
494 al., 2006). Even if some gene regulation can be interpreted as an adaptive mechanism by which  
495 the organism sets up hypoxia-defence processes (e.g., decreased use of energetically costly  
496 metabolic pathways), some may also result in developmental defects. It is therefore likely that  
497 a hypoxic event experienced during early life stages may induce effects during an organism's  
498 entire development that may result in long-lasting modifications in phenotype and in altered  
499 life trajectories (Nettle and Bateson, 2015; Pelster, 2002).

500

501         As far as we know, compared with research on temperature, only a few studies have  
502 examined the long-term effects of early hypoxia events (Fig. 1). While experiments on zebrafish  
503 have shown some instances of adaptive developmental plasticity to hypoxia at subsequent  
504 developmental stages following exposure in early life (Robertson et al., 2014), recent studies

505 on a marine species (European sea bass) produced more ambiguous data (Cadiz et al., 2017;  
506 Vanderplancke et al., 2015; Zambonino-Infante et al., 2017). Therefore, depending on the  
507 intensity and duration of the early constraint, as well as on the developmental window at which  
508 it occurs, low dissolved oxygen levels may disturb energy metabolism and biological processes  
509 involved in organogenesis and morphogenesis of early life organisms that could have short-  
510 and long-term impacts.

511

#### 512 *4.2. Effects of early hypoxia on larval phenotype*

513

514 When black bream embryos were exposed to hypoxia (45–55% DO levels), post-embryos  
515 showed higher deformity rates that could have been related to disturbances in developmental  
516 processes.

517 Such detrimental effects of hypoxia have been suggested to reduce juvenile recruitment in  
518 south-eastern Australian estuaries (Nicholson et al., 2008). In rainbow trout *Oncorhynchus*  
519 *mykiss*, exposure to hypoxia (~34% O<sub>2</sub> saturation) during the embryo stage (from fertilization  
520 until 57 days post fertilization, dpf) induced lower swimming performance in terms of critical  
521 swimming speed, a lower growth rate, and a modified cardiac molecular pattern in resulting  
522 larvae (Johnston et al., 2013). These reduced metabolic and locomotor activities of fish larvae  
523 would make them more vulnerable to predation (Breitburg, 1994; Shoji et al., 2005). It is very  
524 likely that such effects may be common for marine fish species and may have consequences for  
525 later stages in terms of physiological performance and fitness.

526

#### 527 *4.3. Effects of early hypoxia on juveniles and adults*

528

529 Several studies based on laboratory exposure to low DO revealed that hypoxia-induced  
530 developmental plasticity during early stages may result in both adverse and beneficial carry-  
531 over effects on aerobic performance and hypoxia tolerance in fish juveniles.

532 Concerning the adverse effects, a reduced growth rate was measured in European sea bass  
533 juveniles (295–361 dph) that had been exposed to hypoxia (40% saturation) during the larval  
534 stage (30–38 dph) (Cadiz et al., 2018; Vanderplancke et al., 2015; Zambonino-Infante et al.,  
535 2017). Zambonino-Infante et al. (2017) suggested that this growth depression was the  
536 consequence of a reduced efficiency of the protein digestive function. Moreover, Cadiz et al.  
537 (2018) demonstrated that early-life exposure to hypoxia increased glycogen stores, but without  
538 any regulation of carbohydrate metabolism. In European sea bass juveniles, it was also shown  
539 that hypoxia exposure during the larval stage (28–50 dph) induced an irreversible defect in the  
540 formation of the operculum, which negatively influenced the capacity for oxygen extraction of  
541 future juveniles (Cadiz et al., 2018b). This may have further effects on fish metabolism,  
542 including growth rate. More recently, Wood et al. (2017) reported that Atlantic salmon *Salmo*  
543 *salar* juveniles previously exposed to hypoxia (50% saturation) during their early stages (from  
544 fertilization for 100 days) lost equilibrium (i.e. encounter signs of distress) at a higher ambient  
545 dissolved oxygen level compared with those reared in constant normoxia throughout their  
546 development (Wood et al., 2017). These data may have significant implications, since they  
547 suggest that individuals encountering hypoxic waters during early life stages could develop  
548 disadvantageous phenotypes in order to tolerate similar constraints in the future.

549 These maladaptive long-term effects contrast with adaptive developmental plasticity  
550 revealed in zebrafish (Barrionuevo et al., 2010; Robertson et al., 2014). Indeed, early exposure  
551 to low oxygen concentrations has been shown to prepare zebrafish to better cope with hypoxic  
552 conditions at subsequent ontogenetic stages (Barrionuevo et al., 2010; Robertson et al., 2014).  
553 Barrionuevo et al. (2010) showed that adult zebrafish surviving moderate hypoxia (4.3 mg O<sub>2</sub>



554 L<sup>-1</sup> vs normoxia at 7.5 mgO<sub>2</sub> L<sup>-1</sup>) at early life stages exhibited a higher tolerance to hypoxia at  
555 later stages. This was shown by a better aptitude to regulate aerobic and anaerobic capacities  
556 when exposed to acute low oxygen environments. Interestingly, Robertson et al. (2014)  
557 revealed that exposure of zebrafish embryos to hypoxia (0.4 mg O<sub>2</sub> L<sup>-1</sup>) around the time of  
558 cardiac maturation was associated with a male-dominated sex ratio that exhibited higher  
559 tolerance to hypoxia due to lower critical oxygen tension. This result implies both beneficial  
560 and disadvantageous effects, as it would induce a higher tolerance to hypoxia at a later stage,  
561 but also limit reproductive output. These authors explained this result by the significant  
562 induction of the HIF-1 pathway during embryogenesis and suggested that this induction alters  
563 larval tolerance and sex determination. To the best of our knowledge, such developmental  
564 plasticity of hypoxia tolerance following early exposure to low dissolved oxygen has only been  
565 shown in model freshwater fish species.

566         The mechanisms underlying developmental plasticity in marine fish species exposed to  
567 hypoxia are still largely unknown, but are likely similar to the genetic, physiological and  
568 epigenetic factors described in other organisms (Beldade et al., 2011). Investigation of the  
569 effects of early hypoxia exposure during critical windows of development on the subsequent  
570 expression of genes involved in different key physiological/biological processes (e.g.,  
571 reproductive functions, cardiovascular and respiratory functions and metabolic pathways) is  
572 crucial for addressing the mechanisms underlying developmental plasticity. Recent  
573 experiments in European sea bass reveal long-term effects of early exposure to hypoxia on the  
574 regulation of haemoglobin gene expression, suggesting a potential impact on O<sub>2</sub> transport  
575 capacity (Cadiz et al., 2017).

576

577 *4.4. Effects of early hypoxia exposure on later progeny: transgenerational effects*

578

579 Some studies evidenced that parental hypoxia exposure influences the phenotype of their  
580 offspring, even when this exposure was experienced at a very young stage. But, to our  
581 knowledge, only few has been carried out on marine fishes (Lai et al., 2019, 2018; Wang et al.,  
582 2016), and these concern only one species, i.e. the marine medaka *Oryzias melastigma*. In this  
583 species, transgenerational impairments of reproductive function (retarded maturation and sperm  
584 quality, lower hatching success) have been shown on both F1 and F2 generations after parental  
585 exposure to hypoxia throughout their life cycle (15-20% of oxygen saturation) despite these  
586 progenies have never been exposed to hypoxia (Wang et al., 2016). This was associated with a  
587 differential methylation pattern of specific genes involved in cell apoptosis and cycle, as well  
588 as with transcriptomic and proteomic alterations (Lai et al., 2019, 2018).

589 Another study, carried out in freshwater fishes, also reported non-beneficial effects of parental  
590 exposure. Hypoxia exposure of adult carp *Cyprinus carpio* during 8 weeks has been shown to  
591 drastically reduce the larval survival rate of the offspring (20% survival rate measured at 1 mg  
592 O<sub>2</sub> L<sup>-1</sup> vs. 80% survival rate measured at 7 mg O<sub>2</sub> L<sup>-1</sup> i.e. normoxia; Wu et al., 2003). In  
593 zebrafish, the beneficial or non-beneficial nature of parental exposure (13.1 kPa, i.e. about 10-  
594 15% oxygen saturation) has been shown to depend on the duration of this exposure (Ho and  
595 Burggren, 2012). Parental exposure of less than 1 week induced depressed egg component  
596 volume associated with a lower hypoxia tolerance of the offspring. But, when this parental  
597 exposure was longer (more than one week), egg volume returned to the control level, hypoxia  
598 tolerance increased, and longer body lengths were observed for their larval offspring. This  
599 demonstrated the profound epigenetic effects of parental exposure on the morphological and  
600 physiological phenotype of the offspring (Ho and Burggren, 2012).

601

602 *4.5. Conclusions*

603

604 To conclude, the long-term effects of early exposure to low dissolved oxygen are still poorly  
605 documented in marine species. However, current data on European sea bass (Cadiz et al., 2018a,  
606 2018b; Cadiz et al., 2017a, 2017b; Vanderplancke et al., 2015a, 2015b; Zambonino-Infante et  
607 al., 2017), marine medaka (Wang et al. 2016, Lai et al. 2018, 2019) and other model fish species  
608 (Barrionuevo et al., 2010; Ho and Burggren, 2012; Kajimura et al., 2006; Lo et al., 2011;  
609 Robertson et al., 2014) should prompt us to urgently investigate these effects on other marine  
610 species, as the few data existing on marine fish species tend to indicate that development and  
611 transgenerational plasticity to hypoxia leads to maladaptive effects at later stages (Table 1, Fig.  
612 4). While the main observed beneficial effect of early exposure is a higher tolerance to hypoxia  
613 at later stages, most of the other effects observed tend to be non-beneficial and concern mainly  
614 growth, development, and altered sex ratio (Table 1, Fig. 4).

615 Understanding whether early hypoxic exposure sets developmental and transgenerational  
616 plasticity and other long-lasting impacts in marine fish species is crucial to evaluating the  
617 effects of hypoxic events on fish fitness, which determines population structure and dynamics.

618

## 619 **5. Acidification**

620

621 With temperature and hypoxia, increasing mean partial pressure of carbon dioxide  
622 ( $p\text{CO}_2$ ) in the ocean is the third main environmental factor that marine organisms, including  
623 fish, may have to face in the context of global change. Several projections indicate that global  
624  $p\text{CO}_2$  in the oceans will reach 1000  $\mu\text{Atm}$  by 2100, with a corresponding pH decline of 0.4  
625 units (Heuer and Grosell, 2014). However, current  $p\text{CO}_2$  values higher than 1000  $\mu\text{Atm}$  can  
626 already be observed in many coastal zones and estuaries (Melzner et al., 2013).

627 Such  $p\text{CO}_2$  changes directly impact physiological mechanisms controlling gas exchange  
628 in marine fish. Fish exchange  $\text{CO}_2$  across their gills or skin by maintaining a high diffusion

629 gradient with higher pCO<sub>2</sub> values in cells and body fluids compared with the external  
630 environment. Thus, increased pCO<sub>2</sub> in seawater could compromise this exchange, resulting in  
631 hypercapnia (high pCO<sub>2</sub> in blood), which leads to acidosis (Heuer and Grosell, 2014). This  
632 acidosis (in the case of incomplete regulation) or the energetic cost of regulating it (by  
633 bicarbonate buffering and active ion transport) could induce a global metabolic depression with  
634 reduction in growth, survival and negative effects on development for early life stages with  
635 potential effects on later stages (Munday et al., 2009). Because of their high surface-to-volume  
636 ratio and lack of specialized mechanisms for acid-base regulation, embryos and larvae of  
637 marine fish have limited capacity for ion exchange, and are predicted to be more sensitive to  
638 elevated CO<sub>2</sub> than juveniles and adults (Ishimatsu et al., 2008; Kikkawa et al., 2003).

639 While knowledge about impacted physiological functions has grown exponentially  
640 since 2007 (for reviews see Heuer and Grosell, 2014; Kelly and Hofmann, 2013), data about  
641 the effect of early exposure on later stages is lacking, although it is a necessary step to identify  
642 which traits could potentially be under selective pressure or modulated by epigenetic effects  
643 (either by parental effects or the early life environment).

644 In this chapter, we will review to what extent acclimation and exposure to different  
645 ocean acidification (OA) scenarios during early life stages could play a role in mitigating the  
646 effects of this stress and promoting the adaptive capacity of later stages.

647

## 648 *5.1. Effect of early OA on later larval phenotype*

649

### 650 *5.1.1. Adverse effects*

651

652 Several studies performed on different marine fish species revealed skeletal deformities  
653 and, especially, an enlargement of otoliths in young stages exposed to OA (Senegalese sole

654 Pimentel et al. 2014, 2015, white sea bass *Atractoscion nobilis* Checkley et al. 2009; cobia  
655 *Rachycentron canadum* Bignami et al. 2013a, 2013b; mullo way *Argyrosomus japonicus* Rossi  
656 et al. 2016). However, neither the persistence nor the possible consequences of such effects on  
657 later stages have been reported to date. Using a modelling approach, it was suggested that the  
658 increase in otolith size could increase auditory sensitivity, enabling high-pCO<sub>2</sub> exposed fish to  
659 detect sounds that cannot be detected in normal conditions (Rossi et al., 2016). The detrimental  
660 consequence of such increased auditory sensitivity is a susceptibility to respond to disruptive  
661 background noise and incorrectly identify adequate settlement habitats.

662         Similarly, it was reported that elevated pCO<sub>2</sub> (1675 µAtm) induced faster ontogenetic  
663 development in barramundi *Lates calcarifer* larvae but without any earlier onset of orientation  
664 behaviour, which may reduce the chances of larvae finding adequate habitats for settlement,  
665 with potentially serious impacts on subsequent developmental stages (Rossi et al., 2016).  
666 Another recent study on marine medaka *Oryzias melastigma* showed that egg incubation at  
667 moderate (1160 µAtm) or at high pCO<sub>2</sub> (1783 µAtm) did not induce different growth rates,  
668 hatching rates, embryonic duration, or malformation rates (Wang et al., 2017). However, high  
669 pCO<sub>2</sub> level induced longer larvae, and both pCO<sub>2</sub> levels tested induced an alteration in escape  
670 behaviour in terms of C-shape escape response to a stimulus. This suggests altered predator-  
671 prey relationships, with potential long-term effects on fish populations and ecosystem  
672 functioning.

673         All of these studies showed that elevated pCO<sub>2</sub> experienced during the larval stage could  
674 directly impact larval dispersal, survival, and behaviour, which could suggest direct  
675 consequences for animal fitness and population recruitment. However, further longer-term  
676 studies are needed to validate this hypothesis.

677

678 5.1.2. *Coping ability*

679

680 Several examples of coping with OA when experienced from early stages have been  
681 reported in the literature.

682 When embryos of Atlantic herring from the Baltic Sea were exposed to high pCO<sub>2</sub>  
683 (ranging from 1260 to 4635 μAtm) until hatching, there was no effect on development, growth  
684 or otolith size of newly hatched larvae (Franke and Clemmesen, 2011). In addition, no effects  
685 were detected on later swimming and foraging behaviours of Atlantic herring larvae previously  
686 reared in control (370 μAtm), medium (1800 μAtm) or high (4200 μAtm) pCO<sub>2</sub> from the  
687 embryo stage (Maneja et al., 2015), suggesting that Atlantic herring is robust with respect to  
688 OA. Another species, the walleye pollock, *Gadus chalcogrammus*, also seemed to exhibit a  
689 similar coping ability at larval stages in terms of growth potential when exposed to high pCO<sub>2</sub>  
690 values up to 2100 μAtm from the egg stage (Hurst et al., 2013). Increased growth (15–18%  
691 longer and 47–52% heavier) was also reported for clownfish larvae exposed for 11 days after  
692 hatching to pCO<sub>2</sub> ranging from 400 to 1030 μAtm (Munday et al., 2009).

693 Unfortunately, none of the above studies were designed to evaluate possible local  
694 adaptive capacity or long-term effects of early life exposure on later life stage traits and  
695 therefore cannot be used assess the potential “acquired” ability of juvenile fish to cope with  
696 hypercapnia. We need to ask whether developmental acclimation could play a role in allowing  
697 future populations to cope with the behavioural and sensory effects of pCO<sub>2</sub>-induced  
698 acidification. The question is not easily answered, considering that adverse changes occur  
699 rapidly in larvae exposed to elevated pCO<sub>2</sub> levels, with immediate effects on growth and  
700 survival. To help address such points, we recommend using studies with a graduated exposure  
701 approach.

702           Some studies seem to suggest that adaptive capacity by selection of tolerant genotypes  
703 could be an outcome. In this respect, cod larvae from the Norwegian coast exhibited severe  
704 tissue damage to multiple internal organs when exposed to a large spectrum of pCO<sub>2</sub> levels  
705 ranging from 380 to 4000 μAtm, particularly before the onset of acid-base regulation processes  
706 in their gills (Frommel et al., 2011). In contrast, cod from the Baltic Sea seem to be very robust  
707 since no effects were observed on hatching, survival and otolith size during the development of  
708 embryos and larvae exposed to similar increasing pCO<sub>2</sub> ranges (Frommel et al., 2013). These  
709 results are not contradictory since there is an ongoing speciation of the Baltic cod population in  
710 response to local environmental conditions in the Baltic Sea (Berg et al., 2015). Indeed, this  
711 population naturally experiences high pCO<sub>2</sub> and low salinity values during all its life phases  
712 (including the embryo and larval stages), while the Norwegian cod population does not  
713 experience these environmental conditions. These two studies suggest that an acclimation of  
714 each population to their own environment may have resulted in selective pressure in the Baltic  
715 Sea that led to a cod population resilient to acidification. More work is clearly required to  
716 identify which physiological functions are behind this coping ability.

717

## 718 *5.2. Effects of early OA on later progeny: acclimation and transgenerational effects*

719

720           Most studies concerning the effect of early OA exposure on later stages actually concern  
721 transgenerational plasticity (i.e., effects within more than one generation) rather than  
722 developmental plasticity (i.e., effects within one generation).

723           In 2012, Miller et al. demonstrated that the effect of OA on anemonefish *Amphiprion*  
724 *melanopus* physiology was different depending on whether their parents had previously  
725 experienced OA or not. They revealed that juvenile fish descended from parents that had been  
726 conditioned to moderate or elevated pCO<sub>2</sub> levels (581 and 1032 μAtm) exhibited the same

727 growth and survival rates as control fish, while adverse effects were observed in juveniles  
728 whose parents had not been previously conditioned (Miller et al., 2012). On the same species,  
729 Allan et al. (2014) demonstrated that elevated pCO<sub>2</sub> (1087 μAtm vs 400 μAtm for the control)  
730 negatively affected the escape performance of directly exposed juvenile fish in terms of their  
731 reactivity and locomotor performance (decreased speed, response duration and response  
732 distance). However, parental exposure to these same pCO<sub>2</sub> conditions generally reduced these  
733 negative effects, although not completely, indicating the potential for acclimation of  
734 behavioural impairment across generations (Allan et al., 2014). Using an original approach  
735 combining repetitive field sampling with a short-term exposure experiment and parallel  
736 monitoring of the spawning habitat, Murray et al. (2014) observed a tolerance to high pCO<sub>2</sub>  
737 levels (up to 2300 μAtm) in Atlantic silverside progenies when caught late in the spawning  
738 season (Murray et al., 2014). This tolerance, a clear survival advantage, seemed to be induced  
739 by the annual decline in pH observed in the spawning habitat and suggests potential offspring  
740 conditioning brought about by their parent's experience of the acidified environment.

741 Recently, juvenile progenies from CO<sub>2</sub>-tolerant and CO<sub>2</sub>-sensitive spiny damselfish  
742 *Acanthochromis polyacanthus* parents (based on their capacity to detect chemical alarm cues  
743 in high pCO<sub>2</sub> water) were reared at pCO<sub>2</sub> levels of 414 and 754 μAtm, and the transcriptome  
744 of their brains was analysed (Schunter et al., 2016). A differential regulation of most circadian  
745 genes was observed at 754 μAtm in the CO<sub>2</sub>-tolerant progeny, while this regulation did not  
746 occur at 414 μAtm and was not found in CO<sub>2</sub>-sensitive progeny. It was suggested that this  
747 differential regulation could allow a shift in the circadian clock, which could give a  
748 physiological advantage to organisms in fluctuating environments. When faced with OA,  
749 tolerant fish therefore display less pronounced osmoregulatory adjustments and avoid  
750 maladaptive responses to high pCO<sub>2</sub>.



751 These studies clearly indicate that some marine fish have the potential to adjust their  
752 physiology in response to pCO<sub>2</sub>-induced acidification. However, they also underline the fact  
753 that only long-term studies are currently able to reveal such potential, which depends on  
754 parental effects or on early egg/larva conditioning.

755

### 756 5.3. Effects of early OA on later juvenile and adult phenotypes

757

758 A very recent study (Rodriguez-Dominguez et al., 2018) reports the effect of early exposure  
759 to OA on juvenile stages. These authors found evidence that high pCO<sub>2</sub> experienced during the  
760 very sensitive embryonic stage of the benthic scarlet cardinalfish *Vincentia badia* increased  
761 anxiety at a later juvenile stage, which could further impact functions governing population  
762 persistence. Moreover, they showed that this response was not reversed when juveniles were  
763 translocated to control conditions.

764

765 A key physiological function for fitness is reproduction. However, to our knowledge,  
766 nothing is known about how early exposure to acidification could influence this function at  
767 behavioural or mechanistic levels in later stages. At the adult stage, Miller et al. (2013) reported  
768 that breeding activity of cinnamon anemonefish *Amphiprion melanopus* was stimulated after a  
769 9-month period of exposure to different pCO<sub>2</sub> levels ranging from current to expected values:  
770 430, 584 and 1032 μAtm (Miller et al., 2013). Over twice as many fish breeding pairs were  
771 found in the two elevated pCO<sub>2</sub> levels, without any apparent cost to adult body condition,  
772 compared with those exposed to the lowest pCO<sub>2</sub> level (which corresponds to current  
773 environmental levels). Moreover, the increase in reproduction was still more pronounced in  
774 terms of the number of clutches produced in the highest pCO<sub>2</sub> group, without any significant  
775 difference in hatchling length, compared with current levels. Miller et al. (2015) also examined

776 the combined effects of temperature and acidification on adults of the same species.  
777 Surprisingly, they found that pCO<sub>2</sub> and temperature combined had a minimal effect on the  
778 majority of the reproductive traits tested.

779 These contrasting results clearly demonstrate the need to clarify if and how reproductive  
780 performance in marine fish can be impacted by OA, and whether the effects observed on  
781 directly exposed adults would be also observed as a consequence of early exposure.  
782 Specifically, there is a need to know whether there is a pCO<sub>2</sub> threshold (as suggested by Miller  
783 et al., 2015), and if so, whether this threshold is modified according to the ontogenetic stage at  
784 which it is experienced or modulated by the combination of environmental stressors.

785

#### 786 *5.4. Conclusions*

787

788 While a many studies address the effects of OA on marine fish physiology and behaviour at  
789 early stages, only a few concern the long term effect of OA exposure, and these exclusively  
790 examine transgenerational plasticity to study the effect of OA on subsequent generations of  
791 coral reef fishes. It is also necessary, for example, to identify the effect of early OA exposure  
792 on later stages within one generation of a temperate fish. Most studies do not cover such effects.

793 In addition, studies designed to look at the effects of OA within a single stage have mostly  
794 reported the absence of OA effects on fish growth, development, metabolism and swimming  
795 behaviour, which may suggest that marine fish physiology would not be dramatically modified  
796 by OA, at least concerning these performances. However, the design of such studies needs to  
797 incorporate the evaluation of potential local adaptive capacity or long-term effects of early life  
798 exposure on later life stage traits. OA early exposure mainly shows beneficial effects of  
799 developmental plasticity on growth rate and development, which are again found in  
800 transgenerational studies (Fig. 5). Concerning locomotor performance in an OA environment,

801 it is interesting to note that non-beneficial effects of developmental plasticity were reported,  
802 while TGP led to beneficial effects (Fig. 5, Table 1). In addition to focus on the underlying  
803 mechanisms governing developmental and transgenerational plasticity to better understand and  
804 predict such effects, studies in this area should also focus on other key traits related to fitness,  
805 such as reproductive success.

806

## 807 **6. Combined effects of temperature, pCO<sub>2</sub> and hypoxia**

808

809 Experimental studies of environmental factors taken individually provide mechanistic  
810 insights into the effects of such factors on fish physiology, but remain far from the reality of  
811 what happens in marine ecosystems exposed to global change where multiple stressors and their  
812 effects are potentially combined (Fry, 1971). For instance, the solubility of oxygen in water is  
813 strongly temperature dependent (Weiss, 1970), and oscillations of ambient pCO<sub>2</sub> (due to  
814 increased atmospheric pCO<sub>2</sub>) and temperature (global warming) may naturally parallel the  
815 concomitant development of ambient hypoxia (due to eutrophication and stratification  
816 inhibiting oxygen export, Pörtner, 2005).

817 It is difficult to rank or determine the relative importance of the different effects of  
818 climate change on fishes, as they vary greatly among species and even populations. As changes  
819 in temperature are expected to exceed any seen in the past 10,000 years (IPCC, 2013), warming  
820 probably represents the greatest threat for fish (Graham and Harrod, 2009; Pankhurst and  
821 Munday, 2011). However, some interactions between environmental parameters lead to  
822 combined effects on the same physiological mechanisms. Interactions between stressors can be  
823 broadly classified into three types (Folt et al., 1999). (1) Additive effects in which stressors  
824 independently affect an organism such that their combined effects are simply the sum of the  
825 individual effects; this includes instances when one or more stressors do not have a significant

826 effect. (2) Antagonistic effects that occur when one stressor offsets the effect of another. (3)  
827 Synergistic effects that occur when the combined effects of stressors are greater than the sum  
828 of their individual effects.

829         Between 2000 and 2010, 35% of experiments on the effects of climate change involved  
830 two or more stressors (Wernberg et al., 2012). However, only 14% of these studies involved  
831 three or more stressors (Przeslawski et al., 2015) and nearly all were performed on  
832 invertebrates. Very few studies have been dedicated to fish (DePasquale et al., 2015; Jacob et  
833 al., 2002; Kroeker et al., 2013; Zambonino-Infante et al., 2013), and even less have examined  
834 the long-term effects of these combined factors following early exposure (Zambonino-Infante  
835 et al., 2013).

836

### 837 *6.1. Early combined effects of OA, hypoxia, and warming on later stages*

838

839         The early combined effects of OA, hypoxia and warming on later stages urgently needs  
840 to be further investigated to better understand fish responses to global change. Indeed, Pörtner  
841 and Farrell (2008) suggested that warming, increased pCO<sub>2</sub>, and oxygen reduction may exert  
842 synergistic effects on marine fauna by depressing several physiological processes, such as  
843 regulation of acid-base or ionic equilibria, aerobic energy turnover, and protein synthesis  
844 (Portner and Farrell, 2008). By depressing the aerobic rate of an organism, increased pCO<sub>2</sub> and  
845 hypoxia would cause the narrowing of thermal windows (i.e., the temperature range at which  
846 the aerobic metabolism is not limited by the physiological mechanisms of oxygen extraction to  
847 cover oxygen demand), enhancing the detrimental effect of large-scale temperature  
848 fluctuations. This would particularly affect animals living at the extremities of their  
849 temperature-dependent distributions and would result in limited performance and alteration of

850 growth functions. However, very few studies have addressed the combined effect of these three  
851 factors on fish larvae (DePasquale et al., 2015) or their effects at later stages.

852

### 853 *6.2. Combined effects reported on early-life history traits suggest carry-over effects*

854

855 The combined effect of early exposure to OA and hypoxia on later stages has yet to be  
856 tested, but primary studies focusing on a single stage suggest that these factors could induce  
857 long-lasting effects when fish are exposed at young stages. Indeed, DePasquale et al. (2015)  
858 tested the combined effects of high pCO<sub>2</sub> and hypoxia on early-life history traits (time-to-  
859 hatching, hatching success, post-hatch survival, and growth) of three estuarine species, by  
860 exposing them to different conditions at the egg stage and through the early life stages. They  
861 suggested that early life estuarine fish were more sensitive to hypoxia than to low pH conditions  
862 and demonstrated both additive and synergistic negative effects on survival and other fitness-  
863 related traits. There was an additive negative effect on survival and length of inland silverside  
864 *Menidia beryllina*, a seasonal synergistic negative effect on survival of Atlantic silverside  
865 *Menidia menidia*, but no effect on survival of sheepshead minnow *Cyprinodon variegatus*.  
866 These authors suggested that this reduced fitness of fish experiencing both acidification and  
867 hypoxia may limit the productivity of higher trophic organisms that depend on them as prey.

868 Similarly, while not yet studied in the context of developmental or transgenerational  
869 plasticity, the combined effect of OA and temperature is susceptible to induce long-term effects.  
870 European seabass larvae exposed to different temperatures (17°C and 19°C) and levels of pCO<sub>2</sub>  
871 (400 µAtm and 1000 µAtm) showed higher survival and growth under combined warmer and  
872 more acidified ocean conditions, demonstrating a certain coping ability in this environment  
873 (Pope et al., 2014). However, through a meta-analysis of several organisms including fish,  
874 another study revealed a trend towards lower average survival, growth and development upon

875 exposure to elevated pCO<sub>2</sub> and temperature (Kroeker et al., 2013). This is in accordance with  
876 the synergistic decrease in survival and slower development of dragonfish embryos  
877 *Gymnodraco acuticeps* exposed to warming and acidification scenarios, which may induce  
878 changes in phenology (i.e. time of hatching), with further consequences for population  
879 dynamics (Flynn et al., 2015). Nevertheless, these deleterious effects of combined warming and  
880 acidification were not observed in the acidification environment alone, reinforcing the necessity  
881 to consider environmental factors in a combined manner.

882 To our knowledge, the only study reporting how combined environmental factors  
883 experienced during early ontogeny can affect later stages in marine fish is on European sole  
884 *Solea solea* (Zambonino-Infante et al., 2013). The authors tested whether temperature and  
885 trophic conditions experienced during the larval stage had delayed effects on life-history traits  
886 and resistance to hypoxia at the juvenile stage. They reported that warmer larval temperature  
887 (20°C vs 16°C) had a delayed positive effect on body mass and resistance to hypoxia at the  
888 juvenile stage, suggesting a lower oxygen demand in individuals that had experienced elevated  
889 temperatures during larval stages. They suggested that long-term programming of metabolic  
890 pathways leads to an adaptive regulation of metabolic rates and/or oxygen demand with long-  
891 lasting effects.

892

## 893 **7. Synthesis**

894

### 895 *7.1. General trends of plasticity observed for each of the factors studied*

896

897 This review shows that there is a great heterogeneity in the number of studies conducted  
898 according to the factor being tested (Fig. 1, 2). Temperature is a largely documented factor,  
899 both for developmental and transgenerational plasticity, while hypoxia and increased pCO<sub>2</sub> are

900 less well documented. To our knowledge, studies focusing on the effects of elevated pCO<sub>2</sub> have  
901 only considered transgenerational plasticity and not developmental plasticity within one  
902 generation (Fig. 2, 5). About half of the studies considering the hypoxia factor focus on model  
903 species or freshwater species. Therefore, both increasing pCO<sub>2</sub>, and hypoxia remain to be  
904 investigated, in terms of their effects on developmental plasticity in marine fishes.

905         The present review also demonstrates that according to the factor tested, there is a great  
906 heterogeneity in the effects observed, and whether they have been shown to be more or less  
907 beneficial or non-beneficial for later stages (Fig. 2, Table 1).

908 **Table 1.** Summary of published findings on the carry-over effects of environmental temperature, hypoxia and acidification observed in different  
 909 species, following exposure to these environmental factors at early stages. This table also indicates the potential advantage / benefit or disadvantage  
 910 of developmental plasticity or transgenerational plasticity induced by this early exposure. When this advantage/disadvantage was unclear, the  
 911 potential effects of exposure are indicated between the two columns.

Factor tested	Stage at which exposure occurred	Stage at which effects were observed	Type of effects observed	Species	Potential advantage	Potential disadvantage	References
<b>Temperature tested compared to the control</b>							
+ 2°C	egg	larvae	Limited swimming speed	Atlantic herring <i>Clupea harengus</i>		Could affect predator-prey relationship and foraging behaviour	Batty et al. 1993
+ 2°C	egg	larvae	Reduced swimming performance	Sockeye salmon <i>Oncorhynchus nerka</i>		Could lead to poor schooling behaviour, foraging success, predator avoidance capacity and decreased survivorship and larval growth	Burt et al. 2012
+ 4°C	egg	larvae	Faster larval and juvenile growth	Haddock <i>Melanogrammus aeglefinus</i>	Could reduce predation on the larval stage and promote a higher survival rate		Martell et al. 2005b, 2005a
	egg	larvae	Decreased time spent at each developmental stage Earlier emergence of larvae	Senegalese sole <i>Solea senegalensis</i> Atlantic salmon <i>Salmo salar</i>	Associated with longer larvae and juveniles and higher survival rates		Braun et al., 2013



+ 5°C	egg	larvae	Enhanced swimming capacity	Atlantic herring <i>Clupea harengus</i>	May improve later predator-prey relationships, indirectly promoting growth rate	Johnston et al. 2001
+ 5°C	egg	larvae	Accelerated development of notochord and muscle	Atlantic cod <i>Gadus morhua</i> Atlantic salmon <i>Salmo salar</i> Senegalese sole <i>Solea senegalensis</i>	May enhance swimming performance	Hall & Johnston, 2003 Johnston, 2001 Johnston, 2006 Campos et al. 2013
+3 to 6°C	egg	Juveniles	Advanced development of fins	Atlantic herring <i>Clupea harengus</i>	Impact on locomotor behaviour	Johnston et al. 1998
+5°C	Egg & larvae	Juveniles	Thicker body shape, Fin position affected	Sea bream <i>Sparus aurata</i> Sea bass <i>Dicentrarchus labrax</i> Zebrafish <i>Danio rerio</i>	Impact on locomotor behaviour	Loizides et al. 2014 Georgakopoulou et al. 2007 Georga & Koumoundouros 2010
+1 to 2°C	Gametogenesis, embryogenesis, hatching, larvae	Adults	Male-biased sex ratio	Atlantic silverside <i>Menidia menidia</i> Damsel fish <i>Acanthochromis polyacanthus</i> Several freshwater and seawater fish	Could impact population success	Conover & Kynard 1981 Devlin & Nagahama 2002 Valenzuela et al. 2003 Ospina-Álvarez & Piferrer 2008 Navarro-Martín et al. 2009 Brown et al. 2014 Donelson & Munday 2015 Macqueen et al. 2008
+3°C and -3°C	From fertilization until eyed-stage	3 years adults	Muscle fibre characteristics	Atlantic salmon <i>Salmo salar</i>	Impact on locomotor behaviour	Macqueen et al. 2008

+3 to 6°C	egg	Adults	Fin shape and positions Jaw position	Sea bream <i>Sparus aurata</i>	Impact on locomotor behaviour		Loizides et al. 2014
+6 to 10°C	Pre-hatch period	Adults	Fin shape and positions Gill cover Jaw position	Zebrafish <i>Danio rerio</i>	Impact on locomotor behaviour and metabolic performance		Georga & Koumoundouros, 2010
+3-4°C	Larvae	Juveniles	Decreased number of muscle fibres, sometimes correlated with reduced maximum aerobic capacities	Gilthead sea bream <i>Sparus aurata</i>		Could reduce physiological performance	Garcia de la Serrana et al. 2012
+5°C	Larvae	Juveniles	Reduced muscle development, number of mitochondria and maximum aerobic capacities	Sea bass <i>Dicentrarchus labrax</i>		Could reduce physiological performance	Koumoundouros et al. 2009
+1.5 to 3°C	Parents	Progeny	Reduced aerobic scope in parents	Damselfish <i>Acanthochromis polyacanthus</i>	Fully restored in progeny		Donelson et al. 2011
+ 5°C	Mother	Progeny	Grew better in the environment previously experienced by their mother	Sticklebacks <i>Gasterosteus aculeatus</i>	Buffering of short-term detrimental effect of warming		Shama et al. 2014
+ 5°C and + 10°C	Parents	Progeny	Maximal growth of progeny	Sheepshead minnow <i>Cyprinodon variegatus</i>	Enhanced fitness		Salinas & Munch 2012
+ 5°C	Parents & grand-parents	Progeny	Grew better in the environment previously experienced by their mother at early	Sticklebacks <i>Gasterosteus aculeatus</i>	Buffering of short-term detrimental effect of warming at early stages	Opposite results observed at a later stage in progeny	Shama & Wegner 2014

			stages, but the opposite pattern was observed at later stages				
+1.5°C	Grandparents & parents	Adults	Male-biased sex ratio (40%)	Damselfish <i>Acanthochromis polyacanthus</i>	Sex ratio restored after one generation and for the next two generations		Donelson & Munday 2015
+3°C	Parents	Adults	Male-biased sex ratio (50%)	Damselfish <i>Acanthochromis polyacanthus</i>		Male-biased sex ratio (40%) maintained after one generation	Donelson & Munday 2015
+3°C	Grandparents & parents	Adults	No offspring production	Damselfish <i>Acanthochromis polyacanthus</i>		No reproduction	Donelson & Munday 2015
<b>Hypoxia</b>							
34% DO	Embryos	Larvae	Reduced swimming performance (critical swimming speed) Reduced growth Modified cardiac gene expression	Rainbow trout <i>Oncorhynchus mykiss</i>		May affect predator avoidance, foraging behaviour and fitness	Johnston et al., 2013
45-55% DO level	Embryos	Larvae	Higher deformity rate	Black bream <i>Acanthopagrus butcheri</i>		Have been suggested to reduce juvenile recruitment	Nicholson et al. 2008
0.4 mg L <sup>-1</sup>	Embryos	Adults	Male-dominated sex ratio with higher tolerance to hypoxia	Zebrafish <i>Danio rerio</i>	Could improve hypoxia tolerance	Could limit reproductive output	Robertson et al. 2014
4.3 mg O <sub>2</sub> L <sup>-1</sup> vs normoxia at 7.5 mgO <sub>2</sub> L <sup>-1</sup>	Egg	Adults	Higher hypoxia tolerance	Zebrafish <i>Danio rerio</i>	Better aptitude to regulate aerobic and anaerobic capacities when exposed to acute low oxygen environments at adult stage		Barrionuevo et al. 2010

50%	Embryos and larvae	Juveniles	Reduced hypoxia tolerance	Atlantic salmon <i>Salmo salar</i>		Would influence fitness	Wood et al. 2017
40%	Larvae	Juveniles	Reduced growth rate	European sea bass <i>Dicentrarchus labrax</i>		May affect physiological performance and fitness	Zambonino-Infante et al. 2017 Vanderplancke et al. 2015
40%	Larvae	Juveniles	Defect in the formation of the operculum	European sea bass <i>Dicentrarchus labrax</i>		Would influence capacity for oxygen extraction	Cadiz et al. 2018 b
40%	Larvae	Juveniles	Lower growth rate, increased glycogen stores	European sea bass <i>Dicentrarchus labrax</i>		May affect physiological performance and fitness	Cadiz et al. 2018 a
13,1 kPa (~ 10-15 %)	Parents	Larvae	Depressed egg volume Lower hypoxia tolerance Longer body length	Zebrafish <i>Danio rerio</i>	Reversible negative effect if parental exposure > 1 week		Ho and Burggren 2012
1 mg O <sub>2</sub> L <sup>-1</sup> (~10-15%)	Parents	Larvae	Decreased larval survival rate	Carp <i>Cyprinus carpio</i>		May have consequences on population dynamics	Wu et al. 2003
15-20%	Parents	F1 and F2	Retarded gonadal development, decrease gamete quality	Marine medaka <i>Oryzia melastigma</i>		May affect population dynamics	Wang et al. 2016 Lai et al. 2018, 2019
<b>Acidification</b>							
1160-1783	Egg	Larvae	Altered C-shape response  Similar growth rate as the control	Marine medaka <i>Oryzias melastigma</i>	Similar growth rate, hatch rates, embryonic duration, or malformation rates	Altered predator-prey relationship with potential consequences for population dynamics and ecosystem functioning	Wang et al. 2017
1068 μAtm	Egg	Juveniles	Increasing anxiety	Benthic scarlet cardinalfish <i>Vincentia badia</i>		Not reversible, Can impact population persistence	Rodriguez-Dominguez et al. 2018

1100-2300 μAtm	Parents	Larvae	Tolerance of high pCO <sub>2</sub> levels	Atlantic silverside <i>Menidia menidia</i>	Higher tolerance due to the acidified environment experienced by their parents	Murray et al. 2014
414-754 μAtm	Parents	Juveniles	Transgenerational differential regulation of most circadian genes	Damselfish <i>Acanthochromis polyacanthus</i>	Could facilitate adaptation to OA	Schunter et al. 2016
581-1032 μAtm	Parents	Juveniles	Same growth rate as control groups	Anemonefish <i>Amphiprion melanopus</i>	Early exposure increases OA tolerance concerning growth rate	Miller et al. 2012
1087 μAtm	Parents	Juveniles	Similar escape performance as control	Anemonefish <i>Amphiprion melanopus</i>	Reduced negative effects of high pCO <sub>2</sub> on escape performance due to the high pCO <sub>2</sub> environment experienced by their parents	Allan et al. 2014
<b>Combined Factors</b>						
Combined T°C and hypoxia	Larvae	Juveniles	Warmer larval T°C had a delayed positive effect on body mass and resistance to hypoxia at the juvenile stage	Sea bass <i>Dicentrarchus labrax</i>	Could allow adaptive regulation of metabolic rates and/or O <sub>2</sub> demand with long-lasting effects	Zambonino et al. 2013

913 This review suggests that ability of the marine fishes to cope with warming is better when  
914 parents were previously conditioned (Fig. 2A and 2B). Similarly, the literature tends to report  
915 beneficial effects of transgenerational plasticity concerning OA, but studies concerning  
916 developmental plasticity in response to OA exposure at early stages are still very few.

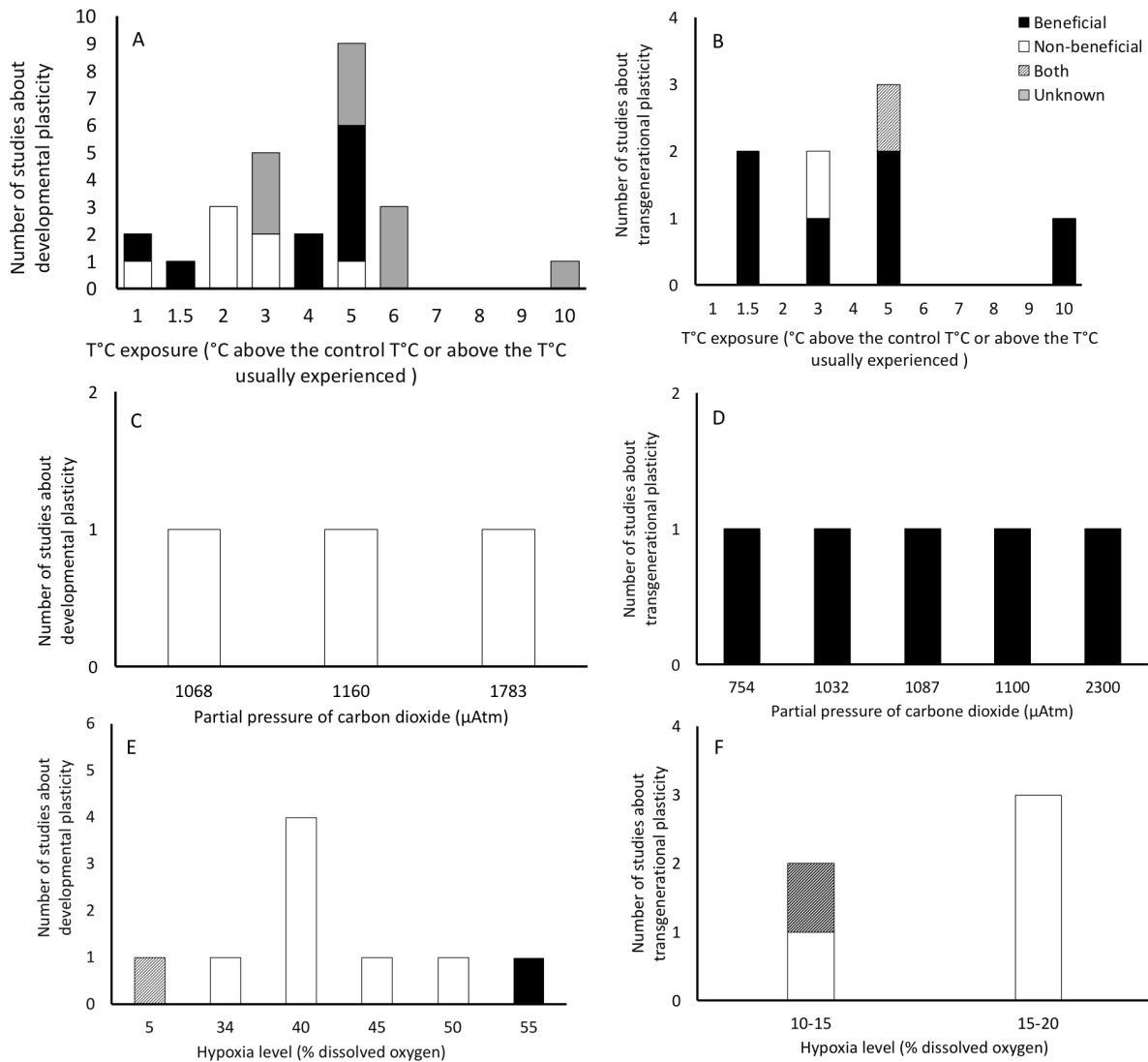
917 Examining the effect of developmental plasticity in fish faced with hypoxia, we can see that  
918 most studies report non-beneficial effects (Fig. 2E), but only one species has yet been  
919 considered for transgenerational plasticity (marine medaka, Wang et al. 2016, Lai et al. 2018,  
920 2019). Therefore, transgenerational studies about hypoxia should be performed to see whether  
921 the trend about beneficial effects would be similar to what we observed for temperature and  
922 OA. In addition, we highly recommend performing transgenerational studies on the effects of  
923 combined factors, as effects could be different when factors are imposed together, than when  
924 tested separately.

925 Nevertheless, it is clear that current studies show that the constraint on testing the effects of  
926 transgenerational plasticity is to work on organisms with short lifespans, limiting the diversity  
927 of species studied. Indeed, among the studies reported here, only six fish species were  
928 examined, and more than 60% of them concerned two coral reef fish species (damselfish and  
929 anemonefish, Table 1). More studies are therefore required to better test transgenerational  
930 effects on longer-lived organisms inhabiting contrasting natural areas (tropical vs temperate for  
931 example).

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Fig. 2



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949 **Fig. 2.** Histograms showing the number of publications reporting effects on later life stages  
950 (beneficial, non-beneficial, both or unknown) via developmental plasticity or transgenerational  
951 plasticity of exposure during early life to warming (A, B) (research papers since 1981);  
952 increased partial pressure of carbon dioxide (C, D) (research papers since 2012); and hypoxia  
953 (E, F) (research papers since 2003) (Cf. Table 1).

954

955

956

957 7.2. *Physiological traits*

958         If we now look at which beneficial and non-beneficial traits are mainly likely to be  
959 induced by a changing environment (Fig. 3, 4, 5), the present analysis shows that the beneficial  
960 effects of warming and acidification mainly concern growth rate and development. Concerning  
961 acidification factor, these beneficial effects were shown both across (TGP) and within  
962 generations (DP), while concerning temperature, they were mostly observed across generations  
963 for growth, and within a generation (DP) for development. Early exposure to hypoxia induced  
964 non-beneficial effects on both growth and development.

965         For both hypoxia and temperature factors, sex ratio and reproductive functions are  
966 among the non-beneficial effects observed (Fig. 3, 4). Further studies are required in order to  
967 see whether these traits relative to reproduction could also be modified by OA through  
968 developmental and transgenerational plasticity, and to what extent it could also be modified  
969 through by combinations of the three factors. For example, would they have a synergistic,  
970 additive or antagonistic effects ration these traits? As mentioned above, their modification in  
971 the natural environment would have many consequences for population dynamics.

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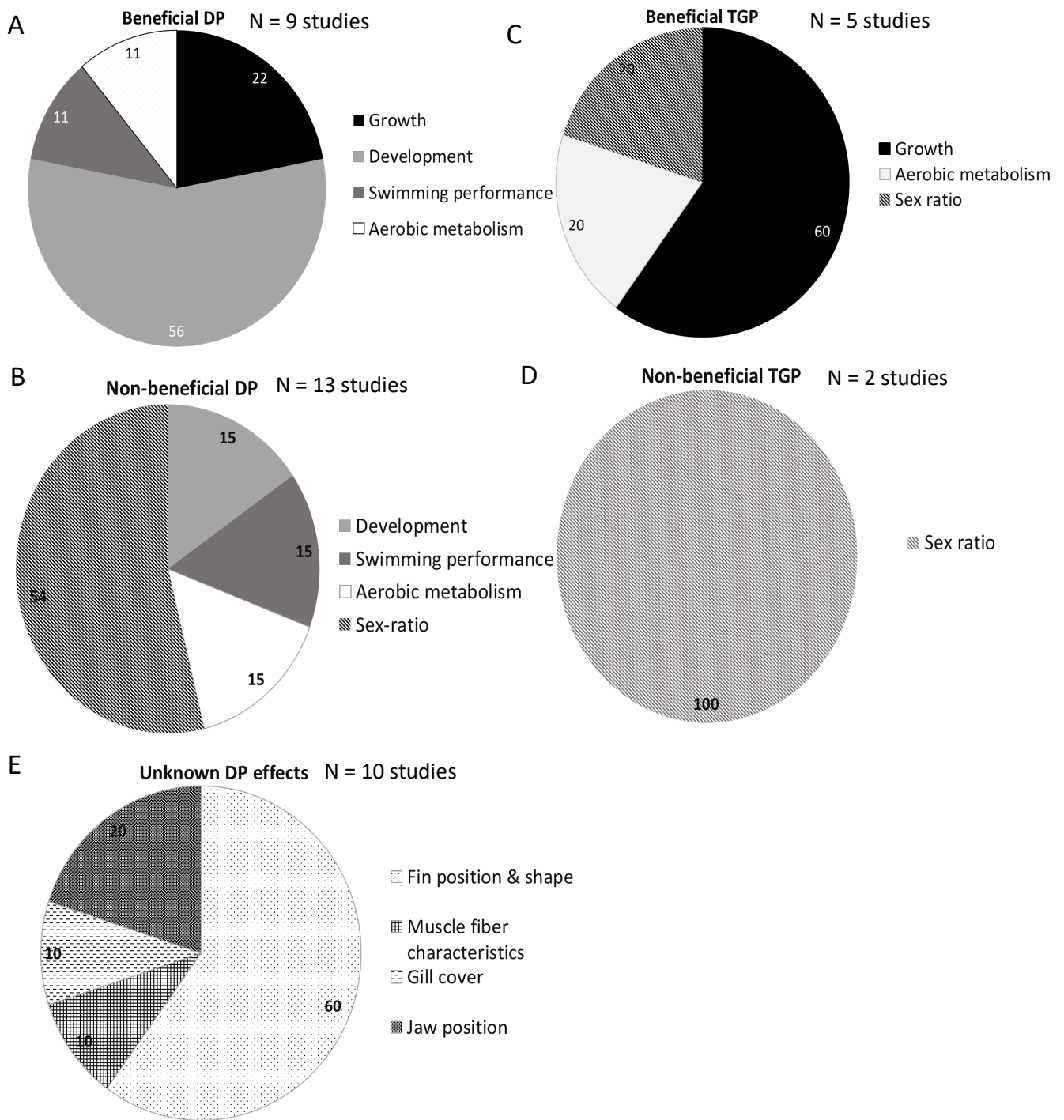
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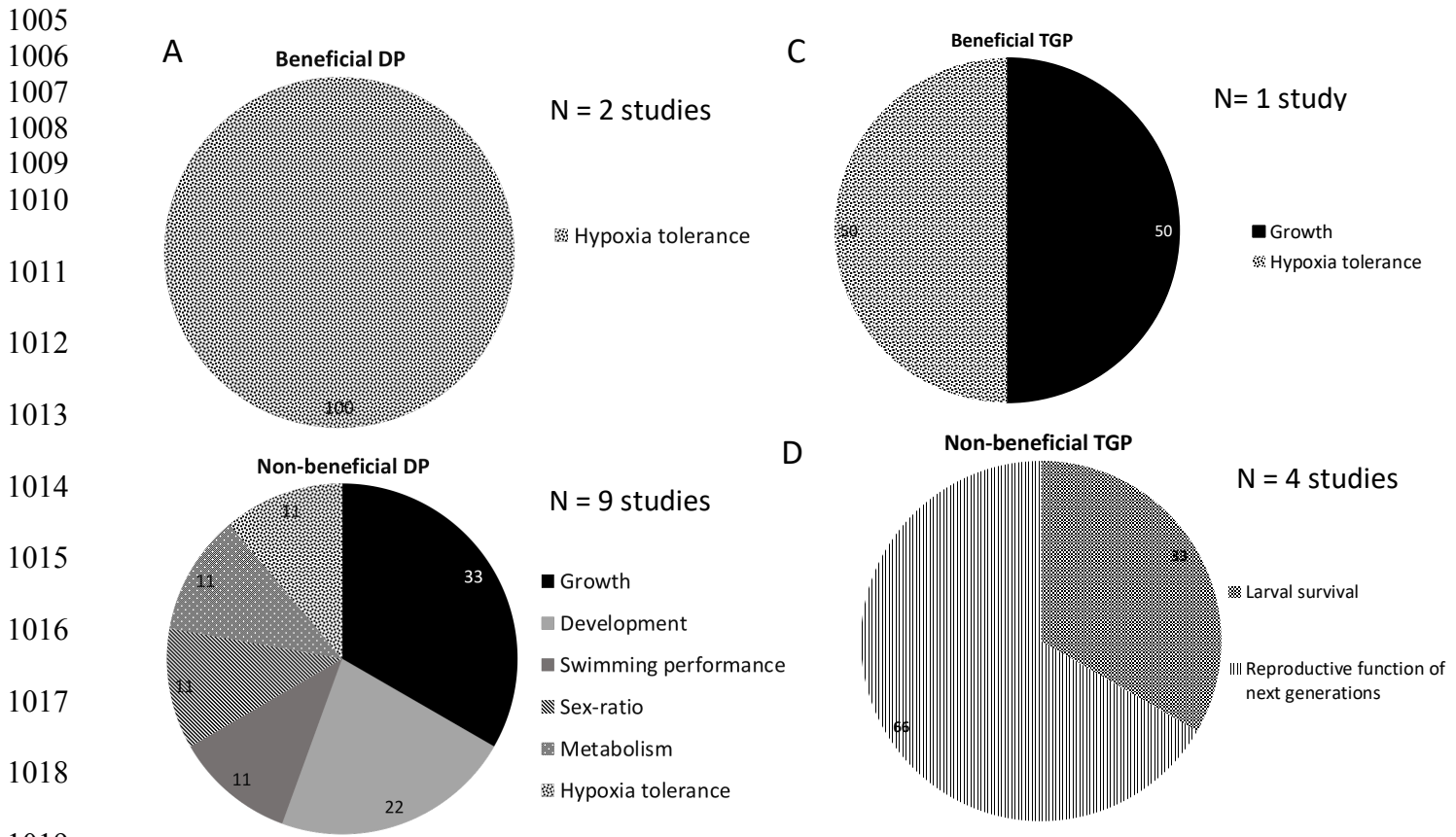
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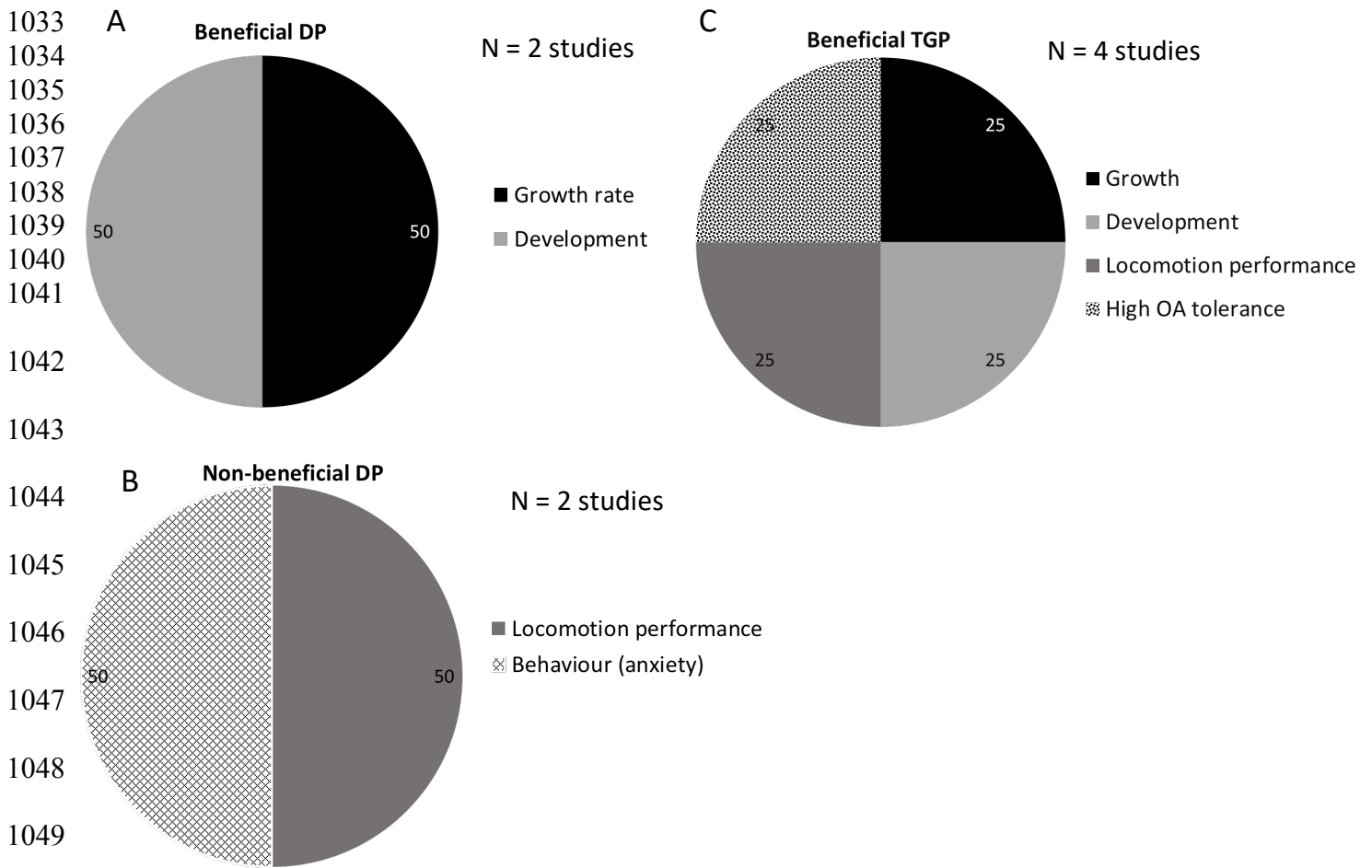
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1000 **Fig. 3.** Diagrams illustrating the numbers of reports in the literature (since 1981) of potentially  
 1001 beneficial, non-beneficial, or unknown subsequent effects of developmental plasticity (DP)  
 1002 (Fig. A, B, E), and transgenerational plasticity (TGP) (Fig. C, D) following exposure to  
 1003 warming (See Table 1). The numbers indicated inside the sectors on each pie chart indicate the  
 1004 percentage of studies.



**Fig. 4.** Diagrams illustrating the numbers of reports in the literature (since 2008) of potentially beneficial (Fig. A, C) and non-beneficial (Fig. B, D) effects of developmental plasticity (DP) and transgenerational plasticity (TGP) following early hypoxia exposure. The numbers indicated inside the sectors on each pie chart indicate the percentage of studies.



1052 **Fig. 5.** Diagrams illustrating the main beneficial (Fig. A, C) and non-beneficial (Fig. B) effects  
1053 of early OA exposure via developmental plasticity (DP) and transgenerational plasticity (TGP)  
1054 reported in the literature since 2012. To our knowledge, no disadvantageous effects of  
1055 transgenerational plasticity have yet been reported. The numbers indicated inside the sectors on  
1056 each pie chart indicate the percentage of studies.

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1062 **8. Conclusions**

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1064 (1) By reviewing how early environmental history can orient later physiological functions of  
1065 fish, this review raises the question of the potential role of early stages in the capacity of fish to  
1066 later adapt to global change. Here, we show that environmental changes occurring during early  
1067 development generally have long-term effects on later stages that can be beneficial or  
1068 detrimental, mainly depending on (i) the developmental window at which the change is  
1069 experienced, and (ii) its magnitude.

1070 (2) Among the three environmental factors studied in this review, hypoxia seems to be the most  
1071 challenging for fish, as most of the effects of early stage exposure lead to negative effects on  
1072 later stages. This hypothesis needs confirmation by complementary research on this factor.

1073 (3) Concerning temperature and OA, most of the studies reveal that adverse effects can be  
1074 reduced after only one generation, demonstrating the plasticity of fish to adapt to a changing  
1075 environment. However, long-term studies across several generations need to be complemented  
1076 by studies on longer-lived species, because current knowledge concerns only short-lived model  
1077 species such as zebrafish, or tropical small fishes, which are not necessarily representative of  
1078 other cases such as, for example, temperate fish species. In addition, the need to pursue and  
1079 expand transgenerational work is all the more crucial as it has been suggested that the  
1080 phenotypic effects of epigenetic changes in response to environmental variations occur  
1081 gradually over several generations (Le Roy et al., 2017).

1082 (4) Establishing the role of early stages in the later capacity of fish to cope with global change  
1083 also requires complementary knowledge of concurrent effects of several environmental factors,  
1084 such as acidification, warming and hypoxia, which are necessary to realistically forecast the  
1085 responses of marine fish. Responses to multiple stressors are poorly understood although crucial

1086 for defining the capacity of fishes to adapt to climate change. Integrated analyses are needed  
1087 based on multiple stressors acting on organisms simultaneously.

1088 (5) This review highlights the generally strong impacts (both beneficial and adverse) of early  
1089 conditioning on later stages and, in this sense, strongly supports the idea that the effect of  
1090 climate change on early life stages of fish is likely to be one of the principle means by which  
1091 climate change affects fish. This was already hypothesized for fishes in coastal waters around  
1092 Great Britain and Ireland (Graham and Harrod, 2009).

1093 (6) We highly recommend stronger interaction between physiologists and modellers for the  
1094 integration of coping ability as a key factor in predictive models of the effect of global change  
1095 on organisms.

1096

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1098

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1102

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