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Fish facing global change: are early stages the lifeline?

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Abstract

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

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

Highlights

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

1. Introduction

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

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

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

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

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

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

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

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

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

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

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

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

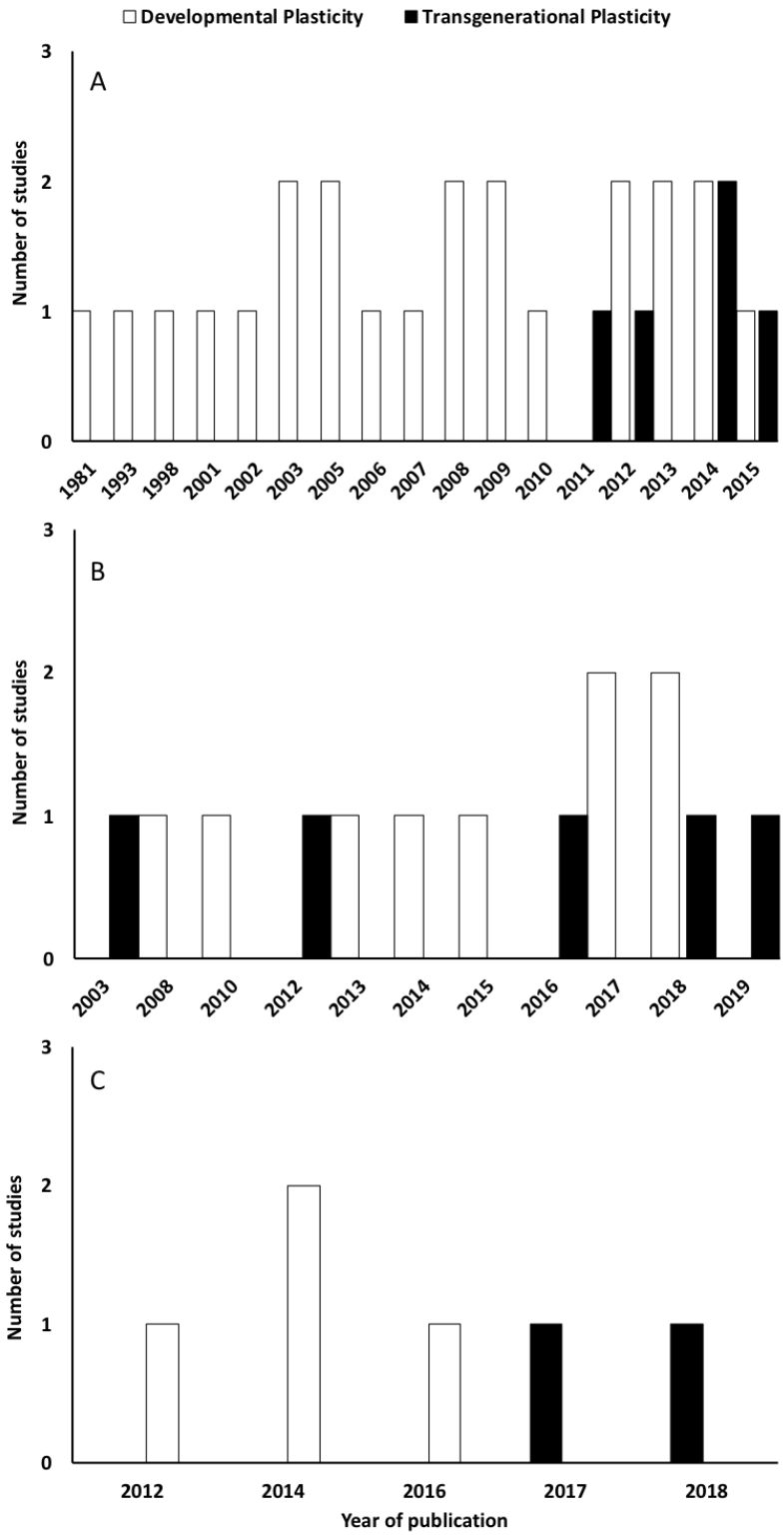

Fig. 1. Distribution of the papers included in the present review across time, environmental factors (A: temperature; B: hypoxia, C: acidification), and type of plasticity (white and black bars respectively represent developmental plasticity and transgenerational plasticity).

3. Temperature

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

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

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

3.1. Effects of early temperature change on larval phenotype

3.1.1. Duration of the larval period

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

3.1.2. Growth, muscle and swimming performance

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

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

The plastic response of myofibrils to a thermal event occurring early in the life history has been widely demonstrated in several fish species and appears to result from a modification of both molecular and cellular processes. Some authors suggested that an increase of 2–3°C in 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)

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

3.2.2. Body shape

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

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

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

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

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

3.3. Effects of early temperature change on adult phenotype

3.3.1. Muscles, body shape, and swimming capacity

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

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

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

3.3.2. Sexual differentiation

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

In many vertebrates, including fish, offspring gender is not immutably determined at fertilization, but instead can be influenced by environmental physical and social conditions experienced during a critical stage of development (during embryogenesis or still later); this is termed environmental sex determination (Angelopoulou et al., 2012; Shine et al., 2002). Among 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

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

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

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

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

3.4.2. Growth and aerobic scope

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

405 Similarly, in stickleback *Gasterosteus aculateus*, 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

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

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

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

One wonders whether progenies acclimated to 1.5°C above their natural current temperature have acquired new “buffering capacities” that would allow them to cope with additional warming episodes, leading to potential transgenerational effects and micro-evolution. Such 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_2) 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_2 is below 2 mg L^{-1}, 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_2 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_2 concentrations, some fish species have developed mechanisms for
473 ambient O_2 sensing and evolved various physiological and behavioural strategies (Jonz et al.,
474 2014). These fish can respond to a decrease in ambient O_2 by trying to escape, increasing
475 ventilation, O_2 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_2-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,

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

4.1. Developmental plasticity at early life stages

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

As far as we know, compared with research on temperature, only a few studies have examined the long-term effects of early hypoxia events (Fig. 1). While experiments on zebrafish have shown some instances of adaptive developmental plasticity to hypoxia at subsequent 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_2 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_2

554 L^{-1} vs normoxia at 7.5 mgO_2 L^{-1}) 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_2 L^{-1}) 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_2 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_2 L^{-1} vs. 80% survival rate measured at 7 mg O_2 L^{-1} 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

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

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

5. Acidification

With temperature and hypoxia, increasing mean partial pressure of carbon dioxide (pCO_2) in the ocean is the third main environmental factor that marine organisms, including fish, may have to face in the context of global change. Several projections indicate that global pCO_2 in the oceans will reach 1000 µAtm by 2100, with a corresponding pH decline of 0.4 units (Heuer and Grosell, 2014). However, current pCO_2 values higher than 1000 µAtm can already be observed in many coastal zones and estuaries (Melzner et al., 2013).

Such pCO_2 changes directly impact physiological mechanisms controlling gas exchange in marine fish. Fish exchange CO_2 across their gills or skin by maintaining a high diffusion

gradient with higher pCO_2 values in cells and body fluids compared with the external environment. Thus, increased pCO_2 in seawater could compromise this exchange, resulting in hypercapnia (high pCO_2 in blood), which leads to acidosis (Heuer and Grosell, 2014). This acidosis (in the case of incomplete regulation) or the energetic cost of regulating it (by bicarbonate buffering and active ion transport) could induce a global metabolic depression with reduction in growth, survival and negative effects on development for early life stages with potential effects on later stages (Munday et al., 2009). Because of their high surface-to-volume ratio and lack of specialized mechanisms for acid-base regulation, embryos and larvae of marine fish have limited capacity for ion exchange, and are predicted to be more sensitive to elevated CO_2 than juveniles and adults (Ishimatsu et al., 2008; Kikkawa et al., 2003).

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

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

5.1. Effect of early OA on later larval phenotype

5.1.1. Adverse effects

Several studies performed on different marine fish species revealed skeletal deformities 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*;* mulloway *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_2 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_2 (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_2 (1783 µAtm) did not induce different growth rates,
668 hatching rates, embryonic duration, or malformation rates (Wang et al., 2017). However, high
669 pCO_2 level induced longer larvae, and both pCO_2 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_2 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_2
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_2 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_2
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_2 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_2-induced
698 acidification. The question is not easily answered, considering that adverse changes occur
699 rapidly in larvae exposed to elevated pCO_2 levels, with immediate effects on growth and
700 survival. To help address such points, we recommend using studies with a graduated exposure
701 approach.

Some studies seem to suggest that adaptive capacity by selection of tolerant genotypes could be an outcome. In this respect, cod larvae from the Norwegian coast exhibited severe tissue damage to multiple internal organs when exposed to a large spectrum of pCO_2 levels ranging from 380 to 4000 µAtm, particularly before the onset of acid-base regulation processes in their gills (Frommel et al., 2011). In contrast, cod from the Baltic Sea seem to be very robust since no effects were observed on hatching, survival and otolith size during the development of embryos and larvae exposed to similar increasing pCO_2 ranges (Frommel et al., 2013). These results are not contradictory since there is an ongoing speciation of the Baltic cod population in response to local environmental conditions in the Baltic Sea (Berg et al., 2015). Indeed, this population naturally experiences high pCO_2 and low salinity values during all its life phases (including the embryo and larval stages), while the Norwegian cod population does not experience these environmental conditions. These two studies suggest that an acclimation of each population to their own environment may have resulted in selective pressure in the Baltic Sea that led to a cod population resilient to acidification. More work is clearly required to identify which physiological functions are behind this coping ability.

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

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

In 2012, Miller et al. demonstrated that the effect of OA on anemonefish *Amphiprion melanopus* physiology was different depending on whether their parents had previously experienced OA or not. They revealed that juvenile fish descended from parents that had been conditioned to moderate or elevated pCO_2 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_2 (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_2 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_2
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_2-tolerant and CO_2-sensitive spiny damselfish
742 *Acanthochromis polyacanthus* parents (based on their capacity to detect chemical alarm cues
743 in high pCO_2 water) were reared at pCO_2 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_2-tolerant progeny, while this regulation did not
746 occur at 414 µAtm and was not found in CO_2-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_2.

These studies clearly indicate that some marine fish have the potential to adjust their physiology in response to pCO_2-induced acidification. However, they also underline the fact that only long-term studies are currently able to reveal such potential, which depends on parental effects or on early egg/larva conditioning.

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

A very recent study (Rodriguez-Dominguez et al., 2018) reports the effect of early exposure to OA on juvenile stages. These authors found evidence that high pCO_2 experienced during the very sensitive embryonic stage of the benthic scarlet cardinalfish *Vincentia badia* increased anxiety at a later juvenile stage, which could further impact functions governing population persistence. Moreover, they showed that this response was not reversed when juveniles were translocated to control conditions.

A key physiological function for fitness is reproduction. However, to our knowledge, nothing is known about how early exposure to acidification could influence this function at behavioural or mechanistic levels in later stages. At the adult stage, Miller et al. (2013) reported that breeding activity of cinnamon anemonefish *Amphiprion melanopus* was stimulated after a 9-month period of exposure to different pCO_2 levels ranging from current to expected values: 430, 584 and 1032 µAtm (Miller et al., 2013). Over twice as many fish breeding pairs were found in the two elevated pCO_2 levels, without any apparent cost to adult body condition, compared with those exposed to the lowest pCO_2 level (which corresponds to current environmental levels). Moreover, the increase in reproduction was still more pronounced in terms of the number of clutches produced in the highest pCO_2 group, without any significant 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_2 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_2 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_2 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_2 (due to
814 increased atmospheric pCO_2) 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_2, 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_2 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_2 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_2
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_2 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_2 are

900 less well documented. To our knowledge, studies focusing on the effects of elevated pCO_2 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_2, 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).

Table 1. Summary of published findings on the carry-over effects of environmental temperature, hypoxia and acidification observed in different species, following exposure to these environmental factors at early stages. This table also indicates the potential advantage / benefit or disadvantage of developmental plasticity or transgenerational plasticity induced by this early exposure. When this advantage/disadvantage was unclear, the 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
Temperature tested compared to the control							
+ 2°C	egg	larvae	Limited swimming speed	Atlantic herring *Clupea harengus*		Could affect predator-prey relationship and foraging behaviour	Batty et al. 1993
+ 2°C	egg	larvae	Reduced swimming performance	Sockeye salmon *Oncorhynchus nerka*		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 Decreased time spent at each developmental stage	Haddock *Melanogrammus aeglefinus* Senegalese sole *Solea senegalensis*	Could reduce predation on the larval stage and promote a higher survival rate		Martell et al. 2005b, 2005a
	egg	larvae	Earlier emergence of larvae	Atlantic salmon *Salmo salar*	Associated with longer larvae and juveniles and higher survival rates		Braun et al., 2013

+ 5°C	egg	larvae	Enhanced swimming capacity	Atlantic herring *Clupea harengus*	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 *Gadus morhua* Atlantic salmon *Salmo salar* Senegalese sole *Solea senegalensis*	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 *Clupea harengus*	Impact on locomotor behaviour		Johnston et al. 1998
+5°C	Egg & larvae	Juveniles	Thicker body shape, Fin position affected	Sea bream *Sparus aurata* Sea bass *Dicentrarchus labrax* Zebrafish *Danio rerio*	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 *Menidia menidia* Damselfish *Acanthochromis polyacanthus* 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
+3°C and -3°C	From fertilization until eyed-stage	3 years adults	Muscle fibre characteristics	Atlantic salmon *Salmo salar*	Impact on locomotor behaviour		Macqueen et al. 2008

+3 to 6°C	egg	Adults	Fin shape and positions Jaw position	Sea bream *Sparus aurata*	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 *Danio rerio*	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 *Sparus aurata*		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 *Dicentrarchus labrax*		Could reduce physiological performance	Koumoundouros et al. 2009
+1.5 to 3°C	Parents	Progeny	Reduced aerobic scope in parents	Damselfish *Acanthochromis polyacanthus*	Fully restored in progeny		Donelson et al. 2011
+ 5°C	Mother	Progeny	Grew better in the environment previously experienced by their mother	Sticklebacks *Gasterosteus aculateus*	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 *Cyprinodon variegatus*	Enhanced fitness		Salinas & Munch 2012
+ 5°C	Parents & grand-parents	Progeny	Grew better in the environment previously experienced by their mother at early	Sticklebacks *Gasterosteus aculateus*	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 *Acanthochromis polyacanthus*	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 *Acanthochromis polyacanthus*		Male-biased sex ratio (40%) maintained after one generation	Donelson & Munday 2015
+3°C	Grandparents & parents	Adults	No offspring production	Damselfish *Acanthochromis polyacanthus*		No reproduction	Donelson & Munday 2015
Hypoxia							
34% DO	Embryos	Larvae	Reduced swimming performance (critical swimming speed) Reduced growth Modified cardiac gene expression	Rainbow trout *Oncorhynchus mykiss*		May affect predator avoidance, foraging behaviour and fitness	Johnston et al., 2013
45-55% DO level	Embryos	Larvae	Higher deformity rate	Black bream *Acanthopagrus butcheri*		Have been suggested to reduce juvenile recruitment	Nicholson et al. 2008
0.4 mg L^{-1}	Embryos	Adults	Male-dominated sex ratio with higher tolerance to hypoxia	Zebrafish *Danio rerio*	Could improve hypoxia tolerance	Could limit reproductive output	Robertson et al. 2014
4.3 mg O2 L^{-1} vs normoxia at 7.5 mgO2 L^{-1}	Egg	Adults	Higher hypoxia tolerance	Zebrafish *Danio rerio*	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 *Salmo salar*		Would influence fitness	Wood et al. 2017
40%	Larvae	Juveniles	Reduced growth rate	European sea bass *Dicentrarchus labrax*		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 *Dicentrarchus labrax*		Would influence capacity for oxygen extraction	Cadiz et al. 2018 b
40%	Larvae	Juveniles	Lower growth rate, increased glycogen stores	European sea bass *Dicentrarchus labrax*		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 *Danio rerio*	Reversible negative effect if parental exposure > 1 week		Ho and Burggren 2012
1 mg O_2 L^{-1} (~10-15%)	Parents	Larvae	Decreased larval survival rate	Carp *Cyprinus carpio*		May have consequences on population dynamics	Wu et al. 2003
15-20%	Parents	F1 and F2	Retarded gonadal development, decrease gamete quality	Marine medaka *Oryzia melastigma*		May affect population dynamics	Wang et al. 2016 Lai et al. 2018, 2019
Acidification							
1160-1783	Egg	Larvae	Altered C-shape response Similar growth rate as the control	Marine medaka *Oryzias melastigma*	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 *Vincentia badia*		Not reversible, Can impact population persistence	Rodriguez-Dominguez et al. 2018

1100-2300 µAtm	Parents	Larvae	Tolerance of high pCO_2 levels	Atlantic silverside *Menidia menidia*	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 *Acanthochromis polyacanthus*	Could facilitate adaptation to OA	Schunter et al. 2016
581-1032 µAtm	Parents	Juveniles	Same growth rate as control groups	Anemonefish *Amphiprion melanopus*	Early exposure increases OA tolerance concerning growth rate	Miller et al. 2012
1087 µAtm	Parents	Juveniles	Similar escape performance as control	Anemonefish *Amphiprion melanopus*	Reduced negative effects of high pCO_2 on escape performance due to the high pCO_2 environment experienced by their parents	Allan et al. 2014
Combined Factors						
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 *Dicentrarchus labrax*	Could allow adaptive regulation of metabolic rates and/or O_2 demand with long-lasting effects	Zambonino et al. 2013

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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

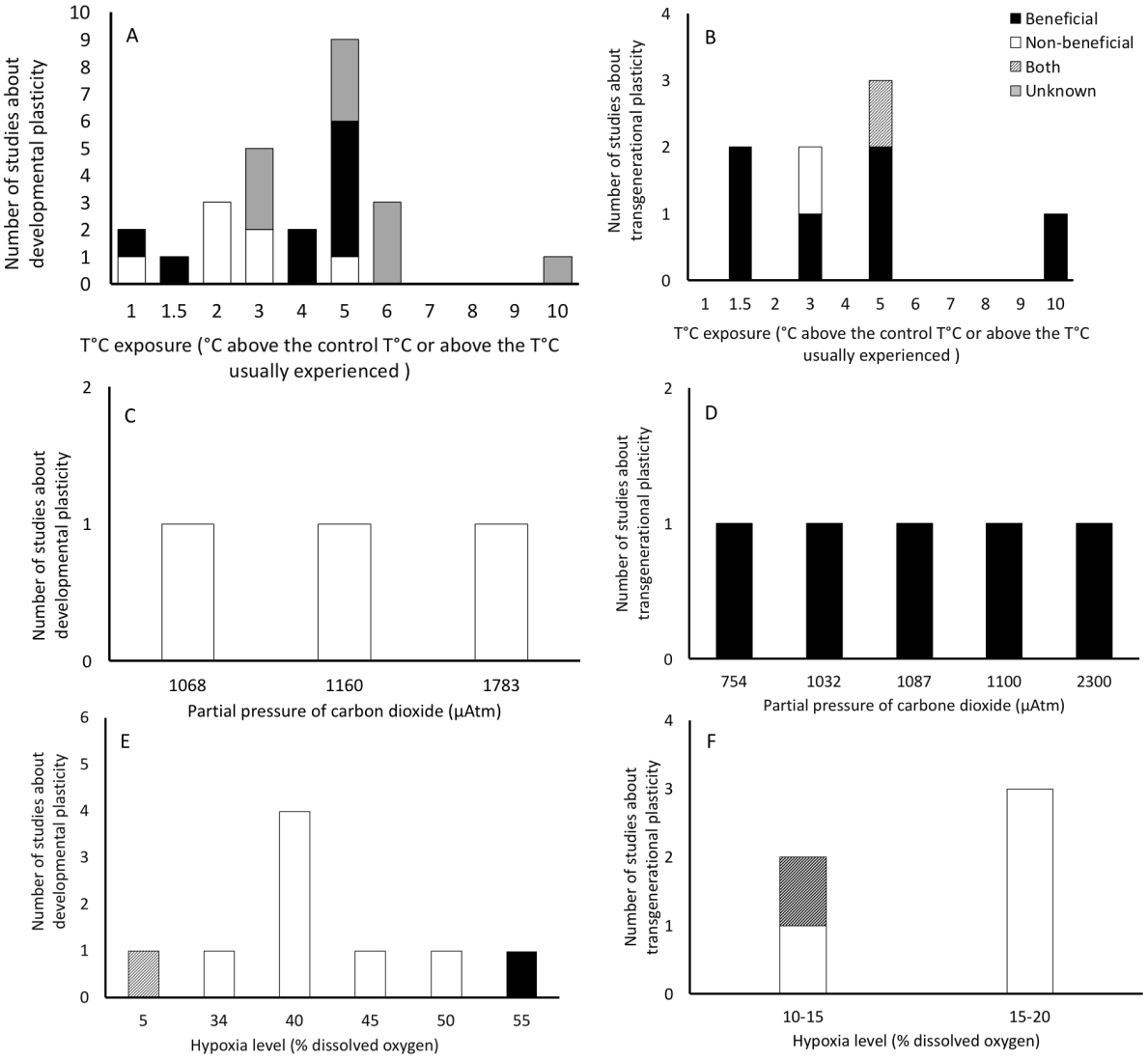

Fig. 2. Histograms showing the number of publications reporting effects on later life stages (beneficial, non-beneficial, both or unknown) via developmental plasticity or transgenerational plasticity of exposure during early life to warming (A, B) (research papers since 1981); increased partial pressure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

7.2. Physiological traits

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

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

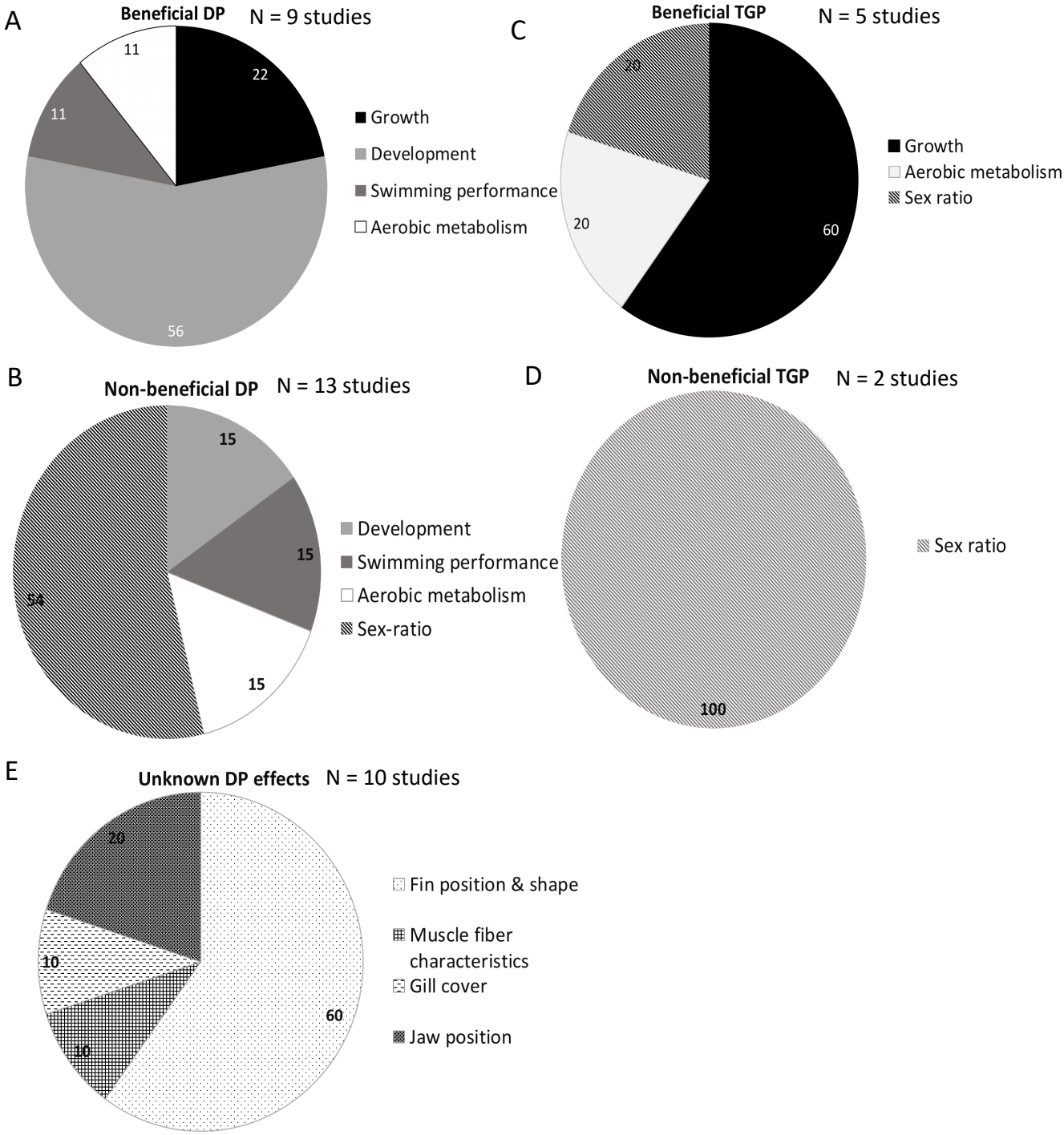

Fig. 3. Diagrams illustrating the numbers of reports in the literature (since 1981) of potentially beneficial, non-beneficial, or unknown subsequent effects of developmental plasticity (DP) (Fig. A, B, E), and transgenerational plasticity (TGP) (Fig. C, D) following exposure to warming (See Table 1).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

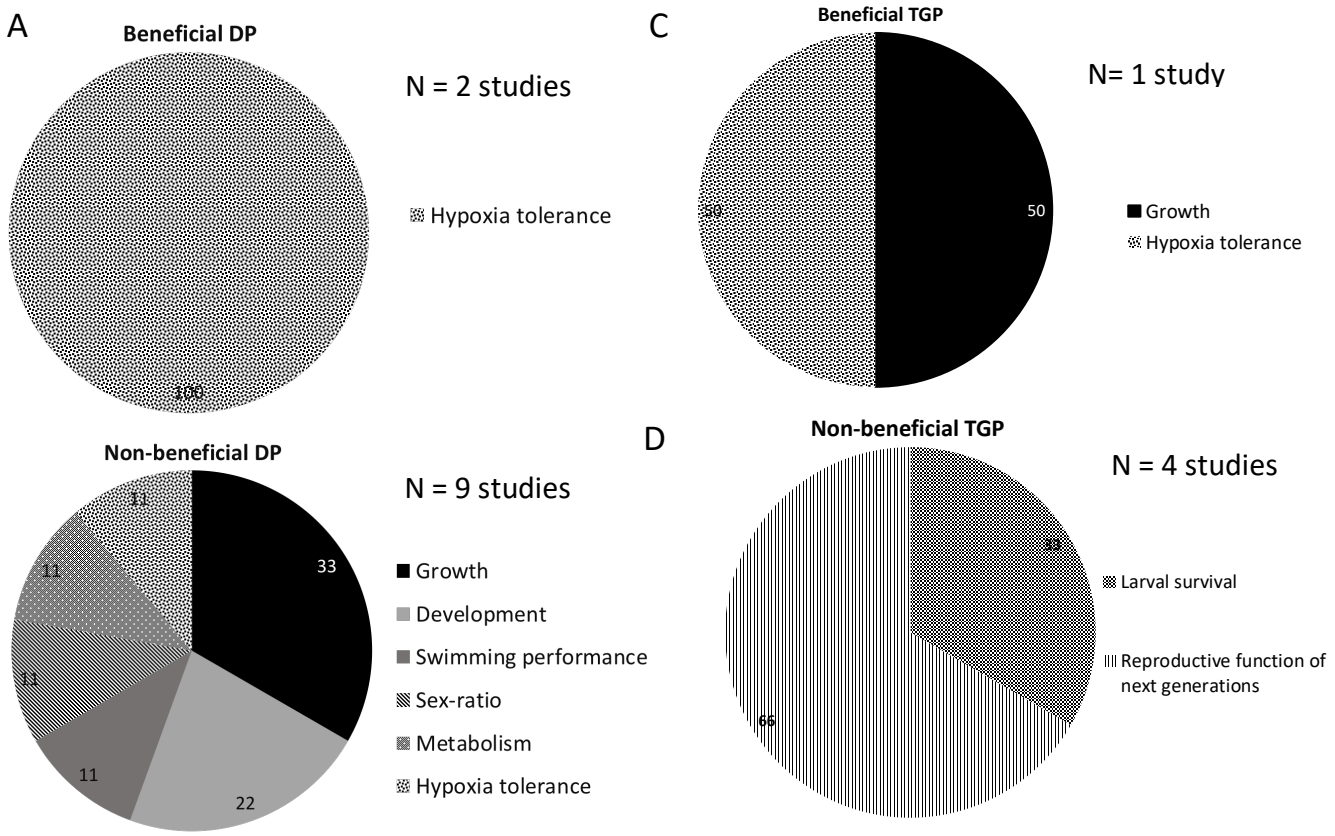

Fig. 4. Diagrams illustrating the numbers of reports in the literature (since 2008) of potentially beneficial (Fig. A, C) and non-beneficial (Fig. B, D) effects of developmental plasticity (DP) and transgenerational plasticity (TGP) following early hypoxia exposure. The numbers indicated inside the sectors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

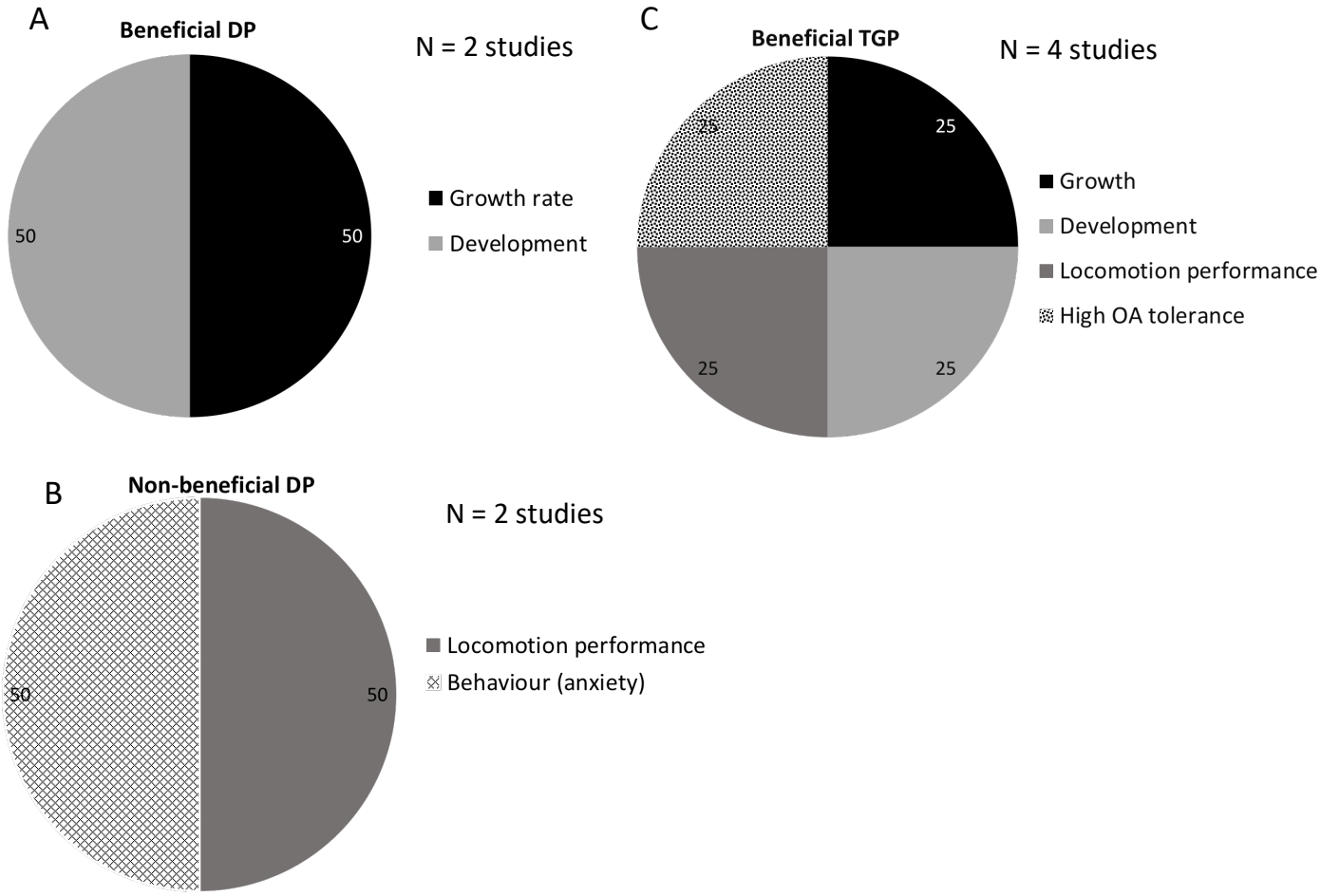

Fig. 5. Diagrams illustrating the main beneficial (Fig. A, C) and non-beneficial (Fig. B) effects of early OA exposure via developmental plasticity (DP) and transgenerational plasticity (TGP) reported in the literature since 2012. To our knowledge, no disadvantageous effects of transgenerational plasticity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

8. Conclusions

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

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

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

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

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

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

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

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