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REVIEW
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Interdependence of Thyroid and Corticosteroid Signaling in Vertebrate Developmental Transitions

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Post-embryonic acute developmental processes mainly allow the transition from one life stage in a specific ecological niche to the next life stage in a different ecological niche. Metamorphosis, an emblematic type of these post-embryonic developmental processes, has occurred repeatedly and independently in various phylogenetic groups throughout metazoan evolution, such as in cnidarian, insects, molluscs, tunicates, or vertebrates. This review will focus on metamorphoses and developmental transitions in vertebrates, including typical larval metamorphosis in anuran amphibians, larval and secondary metamorphoses in teleost fishes, egg hatching in sauropsids and birth in mammals. Two neuroendocrine axes, the hypothalamic-pituitary-thyroid and the hypothalamic-pituitary-adrenal/interrenal axes, are central players in the regulation of these life transitions. The review will address the molecular and functional evolution of these axes and their interactions. Mechanisms of integration of internal and environmental cues, and activation of these neuroendocrine axes represent key questions in an "eco-evo-devo" perspective of metamorphosis. The roles played by developmental transitions in the innovation, adaptation, and plasticity of life cycles throughout vertebrates will be discussed. In the current context of global climate change and habitat destruction, the review will also address the impact of environmental factors, such as global warming and endocrine disruptors on hypothalamic-pituitary-thyroid and hypothalamic-pituitary-adrenal/interrenal axes, and regulation of developmental transitions.

Keywords: thyroid hormones, corticosteroids, hormonal crosstalk, metamorphosis, development, environment, stress

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INTRODUCTION

The hypothalamic-pituitary-thyroid (HPT) axis is the neuroendocrine thyrotropic axis, which literally acts ("trope") on the thyroid gland ("thyro"). In a simplified way, it is composed of brain thyrotropin-releasing hormone (TRH) neurons, pituitary thyrotropin (TSH) cells, and peripheral thyroid hormones (TH), thyroxine (T_4) and triiodothyronine (T_3). TRH acts *via* its receptor

(TRH-R) expressed by the pituitary thyrotropes, and stimulates the synthesis and release of pituitary TSH. TSH binds its receptor (TSH-R) expressed by the thyroid gland to induce the production and release of T_4. At target tissues, T_4 is transformed into T_3 by monodeiodinases, and both bind to TH nuclear receptor, TR. TH can act on various tissues and they negatively feedback on the brain (hypothalamic TRH)/pituitary (TSH) axis (Zoeller et al., 2007).

The hypothalamic-pituitary-adrenal axis (HPA), in mammals and sauropsids, and hypothalamic-pituitary-interrenal (HPI), in amphibians and teleosts, is the neuroendocrine corticotropic axis responsible for the response to stress in all vertebrates (Gorissen and Flik, 2016). The neurohormone, corticotropin-releasing hormone (CRH), controls the production and release of corticotropin (also named adrenocorticotropic hormone, ACTH), at the pituitary level. ACTH acts to control the production and release of corticosteroids (CS) from adrenal cortex cells in amniotes or interrenal cells in amphibians and teleosts. CS can act on various tissues and they negatively feedback on the brain (hypothalamic CRH) / pituitary (ACTH) corticotropic axis (Bernier et al., 2009; Faught et al., 2016; Gorissen and Flik, 2016) *via* specific receptors.

The molecular components of the HPT and HPA/HPI axes have been subject to whole genome duplication (WGD) events during evolution. Two events of WGD, referred to as 1R and 2R for first and second rounds of WGD, occurred in ancestral vertebrates (Dehal and Boore, 2005). An additional WGD event occurred in ancestral teleosts, referred to as 3R for third round of WGD or as teleost specific WGD (Meyer and Schartl, 1999). A further WGD occurred more recently in some teleost groups, such as salmonids (Lien et al., 2016) and some carps (Wang et al., 2012). This event is referred to as 4R (fourth round of WGD). The WGD were at the origin of the diversification of the functions of the HPT and HPA/HPI axis.

One of the actions controlled by the HPT and HPA/HPI axis in vertebrates is the developmental body change coming from a need to adapt to a remarkable change in habitat during birth, hatching or post-embryonic development events. Dramatic changes occur in various metazoa such as cnidaria, insects, crustacean, molluscs, tunicates, and vertebrates. These events have been collectively termed as metamorphosis from the Greek meta- (change) and morph (form). Metamorphosis has a major role in the structure of complex life cycles encompassing different ecophases. In vertebrates, different developmental modes are observed. Amniotes, namely mammals, and sauropsids (birds and reptiles), as well as some amphibians, go through direct development and present a more mature stage at birth/hatching, with an earlier ontogeny of the HPA axis. Non-amniotes, comprising various fish and amphibians, go through indirect development with metamorphosis and present a more immature stage at hatching with a later ontogeny of the HPT and HPA/HPI axis. All the post-embryonic developmental changes are hormonally controlled processes by TH (Paris and Laudet, 2008), but recent studies confer to CS an increasingly prominent role (Sachs and Buchholz, 2017). These TH and CS actions allow to distinguish this period from other major late developmental events such as puberty, which is under the control of sexual steroids.

The post-embryonic developmental transitions are also sensitive to diverse biotic and abiotic factors that can profoundly influence behavior, morphology, growth, development, and sometimes survival. Vertebrates respond to the exposome by modulating the production of CS and TH (**Figure 1**). The adaptive response allows to adjust the timing of the developmental program, but with a trade-off between risk and benefit.

MOLECULAR AND FUNCTIONAL EVOLUTION OF THE HYPOTHALAMIC-PITUITARY-THYROID AND THE HYPOTHALAMIC-PITUITARY-ADRENAL/INTERRENAL AXES AND THEIR INTERACTIONS

Hypothalamic-Pituitary-Thyroid Axis

Thyrotropin-Releasing Hormone and Its Receptors

The hypothalamic-pituitary-thyroid (HPT) axis is the neuroendocrine thyrotropic axis (**Figure 2**). After indirect evidence of the existence of a thyrotropin-releasing factor in dogs (Shibusawa et al., 1955), a fraction, purified from bovine or ovine hypothalamic extracts, was found to stimulate the release of TSH (Schreiber et al., 1961; Guillemin et al., 1962, 1963). The TRH gene encodes multiple identical repeats of the three amino-acid (pyroglutamic acid-histidine-proline) TRH sequence (Galas et al., 2009). This is an example of intragenic duplication which allows an amplification of the synthesis and production of this neurohormone.

TRH-R are members of membrane class A G-protein coupled receptors (GPCR). Two subtypes, TRH-R1 and TRH-R2, have been characterized in mammals. A third one, TRH-R3, has been identified in birds (Li et al., 2020), amphibians (Bidaud et al., 2002), reptiles (Li et al., 2020), and teleosts (Mekuchi et al., 2011; Saito et al., 2011; Li et al., 2020). In birds, only TRH-R1 and TRH-R3 have been identified so far (Li et al., 2020). Four subtypes have been cloned in sockeye salmon *Oncorhynchus nerka* (TRH-R1, TRH-R2a, TRH-R2b, and TRH-R3; Saito et al., 2011), and in medaka *Oryzias latipes* (TRH-R1a, TRH-R1b, TRH-R2, and TRH-R3; Mekuchi et al., 2011). As in medaka (Mekuchi et al., 2011), duplicated TRH-R1a and b are found in many teleosts including zebrafish *Danio rerio*, and might be the result of 3R, even if only one TRH-R1 is identified in sockeye salmon (Saito et al., 2011). The duplicated TRH-R2s present in sockeye salmon may be due to the 4R; TRH-R2b is truncated (Saito et al., 2011). According to the recent hypothesis of Li et al. (2020) on the evolutionary history of TRH-Rs, multiple gene loss events might have occurred during evolution, including TRH-R2 loss in birds, and many mammals, as well as TRH-R3 loss in mammals. Interestingly, pituitary TRH-R3 expression was recently shown to elevate as metamorphosis progressed in bullfrog tadpole (Nakano et al., 2018). It would be interesting to investigate whether the possible involvement of

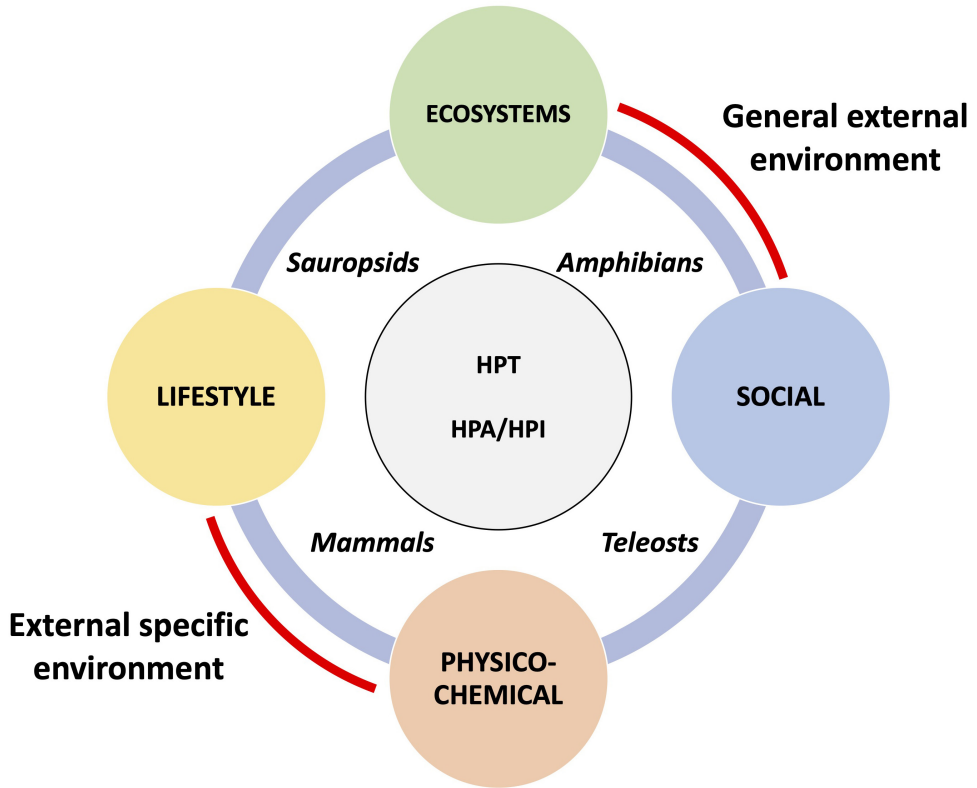

FIGURE 1 | The exposome targets the HPT and HPA/HPI axe in vertebrates. The four components of the exposome (ecosystems, lifestyle, social, and physico-chemical expositions) may affect developmental transitions in vertebrates, including teleosts, amphibians, sauropsids, and mammals, by acting in part at the level of the HPT and HPA/HPI axes.

TRH-R3 in amphibian metamorphosis is also observed in other major life history transitions, such as teleost metamorphoses and sauropsid hatching.

Thyrotropin and Its Receptors

TSH is a glycoprotein hormone composed of two subunits, the alpha subunit (Gpα) common to gonadotropins, and the hormone-specific TSHβ subunit, which is paralogous to the luteinising hormone (LH) and follicle-stimulating hormone (FSH) β subunits. The genes encoding the β subunits of the two gonadotropins LH, FSH and of TSH are paralogous genes that likely arose from the two successive 1R/2R in ancestral vertebrates. A single TSHβ is present in mammals and other tetrapods, as well as in actinopterygians, and is considered as the "classical" TSH. Its β subunit is now named TSHβ1 since a second TSHβ, called TSHβ2, has been identified in some representative species of early vertebrates such as in chondrichthyans and basal sarcopterygians (Maugars et al., 2014). These data suggest that the gene coding for *tshβ2* was lost twice independently during osteichthyan evolution, in a tetrapod ancestor and in an actinopterygian ancestor. Indeed *tshβ2* could not be retrieved in the genome of an holostean (spotted gar *Lepisosteus oculatus*) nor any teleosts, supporting an early loss of *tshβ2* in the actinopterygian lineage, leading to inheritance of only *tshβ1* by the teleost lineage (Maugars et al., 2014). Two *tshβ* paralogs were found in teleosts, resulting from the 3R duplication of *tshβ1* (Maugars et al., 2014; Fleming et al., 2019), and named *tshβ1a* and *tshβ1b* (Fleming et al., 2019). Recently, up to three *tshβ1* paralogs were identified in *Oncorhynchus* species, due to the conservation of the duplicated 4R-paralogs of *tshβ1a (tshβ1aα and tshβ1aβ)* while only the two *tshβ1* paralogs issued from 3R (*tshβ1a* and *tshβ1b*) are present in Atlantic salmon *Salmo salar* as in other teleosts (Fleming et al., 2019). Interestingly, the two *tshβ* paralogs identified in Atlantic salmon are expressed in different pituitary cells (Fleming et al., 2019): *tshβ1a* in the anterior adenohypophysis, and *tshβ1b* in cells near to the pituitary stalk, cells comparable to the *pars tuberalis* TSH cells involved in seasonal physiology and behavior in birds (Yoshimura, 2013) and mammals (Dardente et al., 2019).

TSH-R is present at the surface of the thyroid follicle cells in the thyroid gland. It belongs to the class A GPCR receptors and is paralogous to the receptors for gonadotropins. In teleosts, due to the 3R, duplicated receptors *tshra* and *tshrb* have been characterized (Maugars et al., 2014). TSH-R are not only expressed in the thyroid gland, but also in a variety of other tissues (Williams, 2011). Of particular interest is the presence of *tshr* in the brain and the gonads, where they mediate TSH retrograde action on brain deiodinase and direct regulatory effect on reproduction, in birds and mammals (Nakane and Yoshimura, 2019).

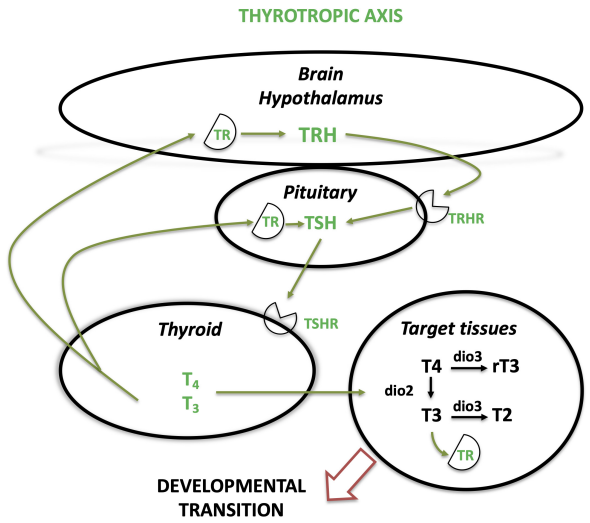

FIGURE 2 | Thyrotropic neuroendocrine axis in vertebrates. The figure displays the main actors of the thyrotropic (hypothalamic-pituitary-thyroid, HPT) axis. dio, deiodinase; T_4, thyroxine; T_3, tri-iodothyronine; rT_3, reverse triiodothyronine; T_2, diiodothyronine; TR, thyroid hormone receptor; TRH, thyrotropin releasing hormone; TRHR, thyrotropin releasing hormone receptor; TSH, thyrotropin; TSHR, thyrotropin receptor.

Thyroid Hormones and Their Receptors

Two main forms of TH are found in vertebrates, T_4 with four iodinated tyrosine residues (3,3′,5,5′), the hormonal precursor produced by the thyroid gland, and T_3 with three iodinated tyrosine residues (3,3′,5), the active hormone which binds to TR with a 10-fold higher affinity compared to T_4 (Holzer et al., 2017). T_4 is produced, by thyrocytes under TSH control, from thyroglobulin, a large dimeric protein containing many tyrosine residues.

TR belong to the nuclear receptor superfamily. Two homologous receptors, TRα and TRβ, are present in tetrapods (Sap et al., 1986; Weinberger et al., 1986; Thompson et al., 1987; Brooks et al., 1989; Helbing et al., 2006; Kanaho et al., 2006). The 3R led to two duplicated *trα* paralogs and two duplicated *trβ* paralogs in basal teleosts, such as conger and eel. So far, four *tr* cDNAs have been cloned in Japanese flounder: two α types and two β types (Yamano et al., 1994; Yamano and Inui, 1995). In some other teleosts, such as zebrafish, two *trα* genes but a single *trβ* gene have been retrieved, suggesting that one of the *trβ* duplicated paralog would have been lost in the course of teleost evolution (Lazcano and Orozco, 2018). *Xenopus laevis* possesses two distinctive genes for each *tr* likely due to its genome polyploidisation (Yaoita et al., 1990). In tetrapods, alternative splicing of TR leads to various protein isoforms with different binding activities and biological functions. In mammals, two TRα variants (α*1* and α*2*) are thus generated from a single gene (Izumo and Mahdavi, 1988). Similarly, in addition to the 3R-duplicated genes, alternative splicing may lead to a large variety of TR isoforms in teleosts, with species-specific variations (Marchand et al., 2001).

Deiodinases

Deiodination of TH corresponds to the removal of iodine from their outer or inner rings, and is performed by iodothyronine deiodinase enzymes in the thyroid, peripheral or central target tissues. By regulating the bioavailability of T_4 and T_3, they thus control their action (Bianco et al., 2002; Orozco and Valverde-R, 2005; Darras and Van Herck, 2012; Orozco et al., 2012; Steegborn and Schweizer, 2020). The first deiodinase to be cloned was *dio1* from rat (Berry et al., 1991), then *dio3* was cloned from *Xenopus laevis* (St. Germain et al., 1994), and *dio2* from *Rana catesbeiana* (Davey et al., 1995). So far, these three types of iodothyronine deiodinases, DIO1, DIO2, and DIO3, have been identified in most vertebrates (Bianco et al., 2002; Darras and Van Herck, 2012; Orozco et al., 2012). DIO1 is a low selectivity enzyme with both outer and inner ring deiodinase activity. DIO2 is an outer ring deiodinase, which removes an iodine residue from T_4 and gives active T_3. DIO3 is an inner ring deiodinase, which inactivates T_4 and T_3 in reverse T_3 (rT_3 or 3,3′,5′-T_3), and diiodothyronine (T_2 or 3,3′-T_2), respectively. Orozco et al. (2012) reviewed the evolutionary history of deiodinase family and point out that *dio1* is the oldest vertebrate deiodinase gene and *dio2* the most recent one. Some teleosts possess 3R-duplicated *dio2* and *dio3* genes (Orozco et al., 2012; Alves et al., 2017). The widespread and differential tissue distribution for the three types of deiodinase in vertebrates has been reviewed previously (Darras and Van Herck, 2012; Orozco et al., 2012). In the Atlantic salmon, up to six deiodinase paralogs have been characterized, one *dio1*, two *dio2* (*dio2a* and *dio2b*) and three *dio3* (*dio3a1*, *dio3a2,* and *dio3b*) (Lorgen et al., 2015). A single *dio2* gene is present in Northern pike *Esox lucius* (Rondeau et al., 2014), which suggests that the two *dio2* paralogs of the Atlantic salmon arose recently from the salmonid-specific WGD, 4R (Lorgen et al., 2015). *Dio3a1*/*3a2* likely also resulted from 4R (Lorgen et al., 2015). Functional divergence of the two salmon *dio2* paralogs is reported: while gill *dio2a* expression is induced by seawater exposure (Lorgen et al., 2015), *dio2b* expression in the brain is sensitive to photoperiod during smoltification (Lorgen et al., 2015; Irachi et al., 2021).

Hypothalamic-Pituitary-Adrenal/Interrenal

Corticotropin-Releasing Hormone and Its Receptors

The hypothalamic-pituitary-adrenal axis (HPA), in mammals and sauropsids, and hypothalamic-pituitary-interrenal (HPI), in amphibians and teleosts, is the neuroendocrine corticotropic axis (**Figure 3**). In 1955, a substance, present in extracts of mammalian hypothalamus and able to stimulate ACTH secretion *in vitro*, was named corticotropin-releasing factor (CRF) (Guillemin and Rosenberg, 1955; Saffran et al., 1955). CRF (or CRH) was first isolated from sheep hypothalamus (Vale et al., 1981) and identified in all vertebrates thereafter (Lovejoy et al., 2014; On et al., 2019). Together with urotensin I (UI) in teleosts, sauvagine (SVG) in amphibians, and urocortins (Ucn) in mammals, it forms a large family of peptides, the CRH/urocortin family. As CRH, urotensin I, sauvagine and urocortins have roles in the regulation of ACTH and MSH, as well as energy metabolism and reproduction (Lovejoy and Balment, 1999). It

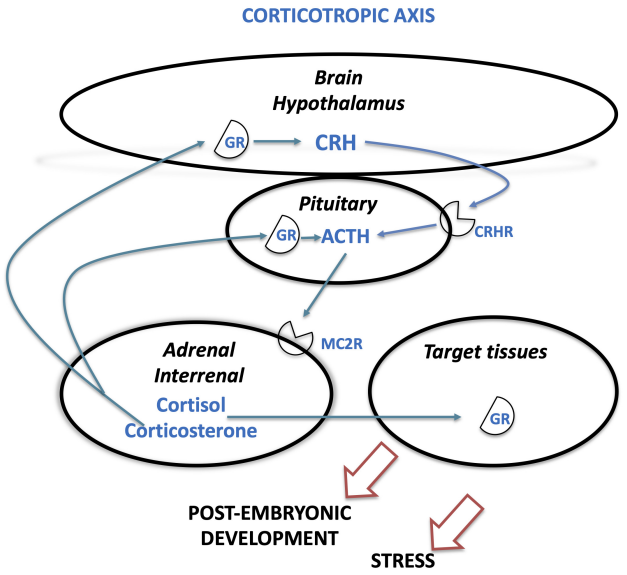

FIGURE 3 | Corticotropic neuroendocrine axis in vertebrates. The figure displays the main actors of the corticotropic (hypothalamic-pituitary-adrenal/interrenal, HPA/HPI) axis. ACTH, adrenocorticotropin; CRH, corticotropin-releasing hormone; CRHR, corticotropin-releasing hormone receptor; GR, glucocorticoid receptor; MC2R, melanocortin receptor 2.

was first suggested that two ancestral *crh/ucn1* and *ucn2/ucn3* genes likely arose by specific gene duplication before vertebrate WGD events (Hwang et al., 2013), as a single crh-like gene is identified in amphioxus and tunicates (On et al., 2019). Both ancestral genes were duplicated twice in ancestral vertebrates *via* 1R and 2R, followed by some paralog losses, leading to up to 5 genes (*crh1, crh2, ucn1* coming from ancestral *crh/ucn1*; *ucn2, ucn3* issued from ancestral *ucn2/ucn3*) in extant representative species of some vertebrate lineages such as chondrichthyans, holosteans and actinistians (Cardoso et al., 2016; On et al., 2019). Teleost specific 3R resulted in the duplication of *crh1* into two paralogs *crh1a* and *crh1b* conserved in many species (Grone and Maruska, 2015; Cardoso et al., 2016). *Crh2* may have been lost in recent teleosts (Cardoso et al., 2016), while one 3R-*crh2* paralog has been conserved in basal groups of teleosts such as European eel (Maugars et al., 2016).

In tetrapods, CRH has been shown to act *via* two GPCRs, corticotropin-releasing hormone receptors (CRHR), CRHR1, and CRHR2, which belong to the class 2 subfamily B1 of secretin-like GPCR superfamily (Lovejoy et al., 2014). *Crhr1* was duplicated by 3R into two paralogs (*crhr1a* and *crhr1b*) which were conserved in many extant teleosts, while one of 3R-duplicated *crhr2* paralogs would have been lost (Cardoso et al., 2016). A third CRHR, CRHR3, identified in the catfish, *Ameiurus nebulosus* (Arai et al., 2001), highly similar to catfish CRHR1, likely results from gene-specific duplication, that may also occurred in various teleosts (Lovejoy et al., 2014; Cardoso et al., 2016).

Proopiomelanocortin-Derived Peptides and Their Receptors

The main pituitary hormone involved in the HPA/HPI axis is ACTH. ACTH is derived from tissue-specific post-translational processing of its precursor, the proopiomelanocortin (POMC); POMC also gives rise to melanocyte stimulating hormone (MSH), and β-endorphin (β-END). POMC forms the opioid/orphanin gene family together with proenkephalin, prodynorphin and proorphanin (Dores et al., 2002; Sundström et al., 2010). ACTH and MSH, called melanocortins (MC), act *via* MC receptors (MCR), while β-END acts *via* opioid receptor. Teleost 3R gave rise to *pomc* gene duplicates: *pomc*-α (*a* or *A*) and *pomc*-β (*b* or *B*), with *pomc*-β having lost a functional β-endorphin (De Souza et al., 2005). Further independent gene-specific duplications during teleost evolution resulted in duplicates of *pomc*-α, such as in sea bream *Sparus aurata* (Cardoso et al., 2011) and *Astatotilapia burtoni* (Harris et al., 2014).

Melanocortin receptors (MCR) belong to the rhodopsin class A13 family of GPCRs. In tetrapods, five MCR genes have been identified: *mc1r* to *mc5r* (Cortés et al., 2014; Dores et al., 2014). In teleost fish, probably due to 3R, the number of receptors increases up to six in zebrafish, which has two MC5R paralogs (Västermark and Schiöth, 2011), while pufferfish *Fugu rubripes* has only four, with no *mc3r* and only one copy of *mc5r* (Logan et al., 2003). Concerning the ligand selectivity of MCRs, all of the paralogous MCRs can be activated by both ACTH and MSH in extant cartilaginous fishes, while in extant teleosts and tetrapods, only ACTH can activate MC2R (Cortés et al., 2014; Dores et al., 2014). In mammals, the MCRs have distinct tissue expression (Cone, 2006; Dores et al., 2014): *mc1r* is mainly expressed in melanocytes; *mc2r* in adrenal cortex; *mc3r* and *mc4r* in the brain; and *mc5r* in a variety of exocrine glands, such as sebaceous, lacrimal and preputial glands. In concordance with their expression sites, each MCR has its proper function: MC1R is involved in skin and hair pigmentation; MC2R in adrenal steroidogenesis and stress response; MC3R and MC4R in energy homeostasis; and MC5R in exocrine gland secretion. These features can also be observed in non-mammalian vertebrates, with some differences. Of particular interest, *mc5r* is co-expressed with *mc2r* in the interrenal of *Xenopus tropicalis* (Dores and Garcia, 2015) and several teleosts [rainbow trout *Oncorhynchus mykiss* (Haitina et al., 2004; Aluru and Vijayan, 2008); common carp *Cyprinus carpio* (Metz et al., 2005); barfin flounder *Verasper moseri* (Kobayashi et al., 2011)], as well as in the chicken adrenal (Takeuchi and Takahashi, 1998), suggesting a possible role of MC5R, in addition to MC2R, in the regulation of HPI axis in these non-mammalian vertebrates.

Corticosteroids and Their Receptors

Corticosteroids (CS) are steroid hormones, divided into glucocorticoids (GC), and mineralocorticoids (MC). In mammals and sauropsids, CS are synthetized by the adrenal gland. In amphibians and teleosts, CS are synthetized by the interrenal gland, a tissue embedded inside the anterior part of the kidney (head kidney) and homologous to the adrenal cortex of the adrenal gland in mammals (Chester-Jones, 1987). Cortisol

is the primary GC in most mammals and teleosts, while it is corticosterone in birds, reptiles, amphibians and many rodents (Mommsen et al., 1999; Aerts, 2018). Both GC can co-exist in most vertebrates. Aldosterone, which is the principal MC in mammals (Gilmour, 2005), is lacking in all teleosts studied so far. In teleosts, it is generally accepted that cortisol plays both GC and MC roles (McCormick, 2001; McCormick et al., 2008).

GC and MC receptors (respectively, GR and MR) belong to the nuclear receptor superfamily. 2R resulted in the emergence of GR and MR, present in all extant vertebrates. In teleosts, 3R gave rise to duplicated *gr* and *mr* (Bury, 2017). Zebrafish is the only known teleost to have conserved only one of the two *gr* paralogs (Schaaf et al., 2008). The two *mr* paralogs are present in a basal teleost, the European eel *Anguilla anguilla* (Lafont et al., 2014), while only one *mr* paralog has been conserved in the other extant teleosts studied so far (Baker and Katsu, 2019).

METAMORPHOSES AND OTHER DEVELOPMENTAL TRANSITIONS IN VERTEBRATES AND THEIR CONTROL BY THYROID HORMONES AND CORTICOSTEROIDS

Larval Metamorphosis in Anuran Amphibians

Involvement of Thyroid Hormones

After hatching and a period of growth, the tadpole undergoes a rapid and irreversible physiological, anatomical and environmental transition marking the transition from the larval state to the adult state, the metamorphosis. Gudernatch observed that the administration of extracts of the thyroid gland (and only this organ) *via* the water induced tadpole premature metamorphosis (Gudernatch, 1912). Following TH measurements (Leloup and Buscaglia, 1977), the elucidation of the roles and mechanisms of action of TH in vertebrates has thus benefited enormously from amphibian model (Grimaldi et al., 2013; Buchholz, 2017; Sachs and Buchholz, 2017). The activity of TH is regulated locally by deiodinases (DIO) and cytosolic proteins (Shi et al., 1994). In particular, the expression of DIO2 (enzyme activating TH) is high in tissues undergoing metamorphosis, while the expression of inactivating deiodinase (DIO3) is high in tissues before and after metamorphosis (Leloup et al., 1981; Galton, 1989).

Another level of TH signaling control is linked to the expression profiles of thyroid hormone receptors (TR) (Yaoita and Brown, 1990). A dual role of thyroid signaling was proposed (Sachs et al., 2000; Grimaldi et al., 2013; Buchholz and Shi, 2018). Thus, before metamorphosis, the relative absence of TH and the expression of TRα contribute to repressing target genes allowing tadpole growth. During the climax of metamorphosis, the high concentration of TH concomitant with the expression of TRα and TRβ contributes to the activation of the transcriptional program leading to tadpole transformation. The two TR isoforms have also different roles during metamorphosis. TRα was shown to be more involved in cell proliferation while TRβ in cell differentiation and apoptosis (Furlow and Neff, 2006; Denver et al., 2009). TRα is required for TH-dependent neurogenesis (Wen et al., 2019). The autoinduction of TRβ is one of the earliest responses to the thyroid signal (Yaoita and Brown, 1990) because *trβ* is a direct TH-target gene (Ranjan et al., 1994; Bilesimo et al., 2011).

Transgenic studies in *Xenopus laevis* revealed that TR are necessary and sufficient for mediating the effects of T_3 during metamorphosis (Buchholz et al., 2003, 2004). However, recent gene knockout studies in *Xenopus tropicalis* showed that TR are not required for most metamorphic transformations, although tadpoles lacking TR die in the middle of metamorphosis (Shi, 2021). Removal of TR enables premature metamorphosis of several adult tissues (Buchholz and Shi, 2018), likely due to the absence of T_3-inducible gene repression. This result supports the role of unliganded TR to avoid precocious metamorphosis for proper tadpole growth. Finally, removal of TR prevents the disappearance of tadpole-specific tissues (Shibata et al., 2020, 2021).

Involvement of Corticosteroids

Glucocorticoids (GC) are also essential during anuran metamorphosis. In *Xenopus laevis* tadpoles, corticosterone concentration is high during pre-metamorphosis, decreases during pro-metamorphosis and increases again during metamorphic climax (Jaudet and Hatey, 1984; Jolivet-Jaudet and Leloup-Hâtey, 1986; Kloas et al., 1997; Glennemeier and Denver, 2002). However, the actions of GC on anuran development are difficult to dissect because of their involvement in many biological processes. Thus, GC inhibit growth, both in pre- and pro-metamorphic tadpoles and the administration of exogenous GC to pre-metamorphic tadpoles inhibits the emergence of lower limbs (Kobayashi, 1958). However, the use of drugs which antagonize the molecular action of GC or prevent the production of GC by the adrenals, inhibits metamorphosis (Kikuyama et al., 1982).

During metamorphosis, GC act through glucocorticoid receptors (GR) that have dynamic and tissue-specific expression profiles (Krain and Denver, 2004). In the tail, GR expression follows the concentration profile of GC, but in the gut and brain the number of transcripts were constant during pro-metamorphosis, and slightly decreased or increased, respectively, during climax. GR knockout in *Xenopus* leads to complete abrogation of the corticosterone-responsive gene induction by exogenous hormone (Sterner et al., 2020). In addition, tadpoles lacking GR developed faster than wild-type sibling until forelimb emergence. Then, they developed more slowly and died at the climax of metamorphosis, indicating that GR is required for metamorphosis and control the developmental rate. The essential requirement of the HPA axis was confirmed with the gene-editing disruption of the *pomc* gene (Sterner et al., 2020). Mutant tadpoles had a reduced level of plasma corticosterone at metamorphosis, as well as lower expression of the corticosterone-responsive genes. Last but not least, these tadpoles had reduced rates of growth and development that finally led to death, late during metamorphosis at the time of tail resorption.

Interactions Between Thyroid Hormones and Corticosteroids

Although TH are the trigger for metamorphosis and are required throughout this process (Sachs and Buchholz, 2017), their actions strongly intersect with those of CS (Sachs and Buchholz, 2019). Stressors such as predation or pond desiccation can be experienced by tadpoles and cause activation of the HPI axis (Glennemeier and Denver, 2002). In the tadpole, the synthesis and release of TSH by the anterior pituitary is under the control of CRH (Denver, 1993, 2021), as in other non-mammalian vertebrates (De Groef et al., 2006). When injected to prometamorphic *Bufo arenarum* larvae, CRH is able to accelerate metamorphosis, likely by direct action on both TSH and ACTH pituitary cells (Miranda et al., 2000). This dual role of CRH allows the tadpole to modulate the rate of metamorphosis in response to environmental stimuli (Denver, 1997). CS are closely linked to metamorphosis by delaying or accelerating its rate of progression. Elevation in circulating CS during the pre-metamorphic stage slows tadpole growth (Denver, 2017). However, during pro-metamorphosis, tadpoles increase the production of TH and CS in response to environmental stress, and are therefore able to accelerate metamorphosis, which can allow the animal to escape a deteriorating larval habitat by transitioning to the next life history stage (Denver, 1997, 2009; Denver et al., 2009; Kulkarni and Buchholz, 2014). Remarkably, CS are capable of triggering metamorphosis in *Buffo boreas* (Hayes et al., 1993). This action is probably due to the endogenous levels of TH with which GC are able to act synergistically, but insufficient, on their own, to induce the metamorphosis.

How does the crosstalk between TH and CS occur? CS are known to promote the expression of activating deiodinases and repress the expression of inactivating deiodinases, thus contributing to the accumulation of active T_3 in target tissues. This model has long been the basis for explaining the potentiating effect of GC on metamorphosis (Galton, 1990). Furthermore, GC can also act in synergy with TH via cross-regulation at the level of their respective nuclear receptors. GC are able to increase the binding capacity of T_3 in cell nucleus (Suzuki and Kikuyama, 1983) and the amount of *tr*β transcripts in the tail, brain and intestine (Bonett et al., 2010). Conversely, the expression of GR seems to be partly controlled by TH depending on the tissues observed: while in the brain and intestine, treatment with T_3 induces a decrease in the expression of GR, the opposite occurs in the tail (Krain and Denver, 2004). These results suggest that CS are able to increase the sensitivity to TH in some tissues, thus accelerating metamorphosis. These actions are synergistic with low concentrations of TH (Bonett et al., 2010). Brown et al. (2014) reported similar hormonal synergy during larval development in fish.

Other genes expressed during metamorphosis are synergistically regulated by TH and CS (Kulkarni and Buchholz, 2012; Bagamasbad et al., 2015), some through direct transcriptional regulation by liganded TR and GR. One of the best studied examples of this type of regulation is the transcription factor krüppel-like factor 9 (Klf9), which is directly and synergistically regulated by TH and CS *via* an ultra-conserved super enhancer located upstream of the transcription start site (Bonett et al., 2009; Bagamasbad et al., 2015). Klf9 strongly enhances TRβ autoinduction in tadpole tissues, among other roles modulating gene transcription and hormone action during metamorphosis (Hu et al., 2016). Other genes show synergistic regulation by TH and CS in tadpole tissues, but whether their protein products function to modulate the rate of metamorphosis requires further study (Kulkarni and Buchholz, 2012, 2014).

Finally, the recent results with tadpoles lacking *pomc* reinforce the inseparable link between TH and GC at metamorphosis (Sterner et al., 2020). Tadpoles lacking *pomc* had reduced expression levels of TH-responsive genes such as *klf9* and *tr*β. Even more significant, mutant death at metamorphosis is rescued by exogenous TH, suggesting a strong entanglement of the signaling by both hormones.

First/Primary and Secondary Metamorphoses in Teleost Fishes

In fishes, two types of metamorphoses can be observed. Both types involve various morphological, physiological and behavioral modifications that preadapt the animal to life in a new environmental niche/habitat, but occur at different life-stages. First/primary metamorphosis typically occurs in elopomorphs and pleuronectiforms, during larval stage and is so-called larval metamorphosis. Secondary metamorphosis occurs in juveniles of some diadromic migratory teleosts and involves less drastic morphological changes. This is the case of smoltification in anadromous salmonids, which allows the transition from a juvenile ecophase in freshwater to the next ecophase in the ocean.

Larval Metamorphosis in Teleosts: The Example of Flatfish

Beside the striking larval metamorphosis in eels and flatfishes, studies also report developmental changes controlled by TH during larval to juvenile transition in various teleosts such as grouper *Epinephelus coioides* (de Jesus et al., 1998), seabream (Campinho et al., 2010), gobiid *Sicyopterus lagocephalus* (Taillebois et al., 2011), or clownfish *Amphiprion percula* (Salis et al., 2021). Our review will focus on the well-known pleuronectiform/flatfish metamorphosis. Larval metamorphosis with the migration of one eye to the opposite side of the head is unparalleled in vertebrate development (Inui and Miwa, 2012). Spectacular morphological changes are accompanied by behavioral (pelagic to benthic life and locomotion) and physiological (such as development of gastrointestinal tract to adapt to the novel food resources in a new habitat) changes.

Involvement of Thyroid Hormones

In the Japanese flounder *Paralichthys olivaceus*, larval tissue T_4 and T_3 concentration increases gradually during pro-metamorphosis, and rises sharply at the beginning of climax, reaching highest level at climax (Miwa et al., 1988; Tanangonan et al., 1989; Tagawa et al., 1990; de Jesus et al., 1991). A similar surge of tissue TH concentration at metamorphic climax is reported in spotted halibut, *Verasper variegatus* (Hotta et al., 2001a,b), Atlantic halibut *Hippoglossus hippoglossus*

(Einarsdóttir et al., 2006), and summer flounder, *Paralichthys dentatus* (Schreiber and Specker, 1998).

Treatments of flatfish by TH or anti-thyroid drug have demonstrated the involvement of TH in many metamorphic changes (Inui and Miwa, 2012). One of the most striking examples concerns skeleton development (shortening of fin rays, eye migration and asymmetry). The elongated fin rays at the anterior end of the dorsal fin shorten to reach similar length to other fin rays. Manipulation of T_4 availability disrupts pre-metamorphic Japanese flounder larvae shortening of elongated fin rays (Inui and Miwa, 1985; Miwa and Inui, 1987; de Jesus et al., 1990). Administration of T_4 to pre-metamorphic larvae accelerates eye migration (Inui and Miwa, 1985; Miwa and Inui, 1987; Solbakken et al., 1999). In addition, Schreiber and Specker showed a stage-specific developmental response to TH, with a more pronounced effect in the induction of eye migration at earlier stages (Schreiber and Specker, 1998). Campinho et al. (2018) gave the first evidence of a TH-responsive asymmetric center located in the anterior head region that is correlated with asymmetric development during metamorphosis of flatfish.

In Japanese flounder, expression of *trαA* and *trβs* (*trβ1* and *trβ2*) genes increase rapidly at metamorphic climax; while expression of *trαA* peaks at climax and decreases thereafter (like T_4 content), expression of *trβs* peak at post-climax and remains high in metamorphosed juveniles; in contrast, expression of *trαB* remains low throughout larval development (Yamano and Miwa, 1998). In the turbot, *Scophthalmus maximus*, *trα*, but not *trβ*, expression is up-regulated at metamorphic climax (Marchand et al., 2004). In contrast, studies in two other flatfishes, the halibut (Galay-Burgos et al., 2008) and the Senegalese sole *Solea senegalensis* (Isorna et al., 2009; Manchado et al., 2009), describe a situation similar to that in amphibian with only *trβ* expression showing a peak during metamorphosis.

DIO2 activity and *dio2* expression increase during sole metamorphosis, while DIO3 activity and *dio3* expression decline at mid-late metamorphic period (Isorna et al., 2009). These developmental profiles of deiodinases coincide with the rise of TH levels observed. In this species, there is an asymmetric expression of *dio2* and *TRβ* in the head, which coincides with the head region where asymmetric development of bone and brain occurs (Campinho et al., 2018). In the Japanese flounder, *dio1* is expressed in liver from pro-metamorphosis to early climax, while *dio2* is expressed in limited regions of the eyes, tectum and skeletal muscle from pro-metamorphosis to post-climax, and *dio3* in skeletal muscle and gastric gland blastemas at metamorphic climax (Itoh et al., 2010).

Involvement of Corticosteroids

Data support a role of CS in larval flatfish metamorphosis. Whole body cortisol concentration in Japanese flounder increases during pro-metamorphic stage, reaching a peak level at climax, and decreases thereafter to about half of the maximal level (de Jesus et al., 1991). *In vitro* cortisol treatment of cultured dorsal ray fins from Japanese flounder is not effective alone on inducing metamorphic-like changes such as resorption of the fin rays (de Jesus et al., 1990). In contrast, *in vivo* cortisol treatment *via* water of pro-metamorphic flounder larvae for 15 days is not able to trigger some of the changes observed during metamorphosis, like settling (benthic) behavior and eye migration, but does induce shortening of second fin ray (de Jesus et al., 1990). Administration of cortisol *via* water to spotted halibut increases the occurrence of ambicolored juveniles by inducing the development of adult type pigment cells on the blind side of fishes (Yamada et al., 2011). In cortisol-implanted juvenile Senegalese sole, hepatic and renal DIO2 activities are enhanced, suggesting that CS can be key regulator of extrathyroidal T_3 production in this species (Arjona et al., 2011). This regulation is likely to occur also during sole larval metamorphosis.

Interactions Between Thyroid Hormones and Corticosteroids

Few data are available concerning the interactions between TH and GC in the control of teleost larval metamorphosis. In the Japanese flounder, a permissive effect of cortisol on thyroid hormone action is observed during metamorphosis (de Jesus et al., 1990). Indeed, cortisol alone does not affect the shortening of fin rays *in vitro*, whereas when added together with T_4 or T_3, it enhances its rate compared to T_4 or T_3 alone. This permissive effect of cortisol on TH action was not reported *in vivo* (de Jesus et al., 1990). Combined T_4 and cortisol treatment does not induce either synergistic effects on settling behavior and eye migration, compared to T_4 treatment alone (de Jesus et al., 1990). The authors concluded that it may be due to sufficient production of endogenous cortisol by larval interrenal. Future studies should aim at investigating the mechanisms of CS/TH interactions in teleost metamorphoses as deciphered in amphibians.

Secondary Metamorphosis in Teleosts: Example of Smoltification in Salmonids

Smoltification is the transition of sedentary juvenile parr into downstream migratory smolt, which will pursue its growth phase in the ocean. Smoltification gathers many changes, morphological ones, such as body silvering and fin darkening, behavioral ones, with swimming activity in open space, formation of schools and downstream migration, and physiological ones related to adaptation to seawater and imprinting (Hoar, 1976, 1988; Boeuf, 1993; McCormick, 2012; Rousseau et al., 2012).

Involvement of Thyroid Hormones

Even if some authors do not consider salmonid smoltification as a metamorphosis (Bishop et al., 2006), this transformation from parr to smolt involves major changes and is necessary for the fish to reach its next habitat and survive in a new environment. Moreover, many parallel features exist between flatfish metamorphosis and salmonid smoltification, as reviewed by Björnsson et al. (2012). Lastly, control by TH is crucial in smoltification.

In salmonids, a rise of plasma T_4 and/or T_3 levels is observed at the time of smoltification (McCormick et al., 2009; Björnsson et al., 2012). Manipulation of TH levels by administration of T_4, T_3 or anti-thyroid drugs supports a major role of TH in many smoltification-related morphological, behavioral and physiological changes, such as metabolism, olfaction, change in visual pigments, swimming behavior and downstream migration (McBride et al., 1982; Rousseau et al., 2012). The examples of TH-induced changes, given here, are necessary for avoiding

predation and for adaptation to a new environment, seawater (SW). A pioneer study showed that intramuscular injection of mammalian thyroid extract or TSH induces silvery smolt stage in rainbow trout (Robertson, 1949). Following studies confirmed that exogenous TH (Miwa and Inui, 1983, 1985; Ikuta et al., 1985; Coughlin et al., 2001) and TSH (rainbow trout: Premdas and Eales, 1976) induce body silvering. The silvering of the body is due to the deposition in the skin of purines, hypoxanthine and guanine, the level of which is increased by T_4 treatment in masu salmon *O. masou* (Ura et al., 1994). Early evidence reported the involvement of TH in salinity preference: TSH-treated coho salmon *O. kisutch* shows a change from freshwater (FW) to SW-preference, while the contrary is observed in pink salmon *O. gorbuscha* treated by an anti-thyroid drug (Baggerman, 1963). Similarly, T_4 treatment increases the salinity preference in coho salmon (Iwata et al., 1990). In Atlantic salmon, T_3 increases SW survival (Saunders et al., 1985).

Interestingly, a large peak of expression of *tshβ1b* during Atlantic salmon smoltification, at the time of the initiation of the downstream migration, has recently been demonstrated, with no change in the expression of the paralog *tshβ1a*, suggesting the involvement of *tshβ1b* at smoltification, possibly in the initiation of migration (Fleming et al., 2019). In addition, the expression of pituitary *tshβ1b*, and not *tshβ1a*, is induced by long day-photoperiod (16h of light and 8h of dark) in Atlantic salmon (Irachi et al., 2021).

Expression of TR has been detected in all the tissues involved in smoltification-related changes (Marchand et al., 2001; Jones et al., 2002; Raine et al., 2005; Harada et al., 2008). Expressions of *trα* and *trβ* show no drastic change between the different stages of smoltification in brain, liver, eyeball, and skin in coho salmon (Harada et al., 2008). In contrast, the olfactory epithelium of masu salmon presents more T3 binding sites at smolt than at parr and pre-smolt stages, suggesting that olfactory tissues may be particularly sensitive to TH, related to a possible role in imprinting of natal stream odors in order to migrate back there to reproduce (Kudo et al., 1994). DIO3 activities are enhanced at smoltification in liver (Eales et al., 1993; Sweeting et al., 1994; Specker et al., 2000) and gill (Sweeting et al., 1994). The expression of one of the 4R-paralog, *dio2b*, increases in the brain in zones of cell proliferation during smoltification in response to photoperiod (Lorgen et al., 2015; Irachi et al., 2021).

Involvement of Corticosteroids

The cells of interrenal tissue undergo hypertrophy during smoltification (for review: (Specker, 1982). Pituitary corticotropic cells are also activated during smoltification in Atlantic salmon (Olivereau, 1975). Plasma cortisol levels are low in winter, increase during spring at the time of smoltification and decline from July to September (Langhorne and Simpson, 1981, 1986; Specker and Schreck, 1982; Barton et al., 1985; Virtanen and Soivio, 1985; Young et al., 1989; Nagae et al., 1994; Sundell et al., 2003). Maximal *in vitro* responsiveness of interrenal tissue to ACTH is observed in April in coho salmon (Young, 1986).

As for TH, we will concentrate on the effects of HPI manipulation on pigmentation and osmoregulation. Injection of ACTH in Atlantic salmon can induce darkening of dorsal, pectoral and caudal fins, but neither ACTH nor cortisol have an effect on body silvering (Langdon et al., 1984). Prolonged cortisol treatment in pre-smolt salmons increase Na^+/K^+-ATPase activity in the gill (Richman et al., 1987; Madsen, 1990) and in gut (Madsen, 1990; Veillette and Young, 2005). *In vitro*, cortisol treatment maintains Na^+/K^+-ATPase activity, which declines in controls, in tissue culture of FW-adapted sockeye salmon intestine (Veillette and Young, 2005). Injections of FW-Atlantic salmon with cortisol increase the expression of claudins (tight-junction proteins) involved in the remodeling of the gill in response to salinity changes (Tipsmark et al., 2009). Using primary cultures of Atlantic salmon gill tissue, a stimulatory effect of cortisol is observed on the expression of claudins; an effect blocked by GR antagonist, mifepristone (or RU486), suggesting the involvement of a glucocorticoid type receptor (GR) (Tipsmark et al., 2009).

An increase in gill GR concentration and *gr* expression is reported during smoltification in all studied salmonid species (McLeese et al., 1994; Shrimpton and Randall, 1994; Shrimpton, 1996; Mazurais et al., 1998; Shrimpton and McCormick, 1998, 2003; Mizuno et al., 2001; Kiilerich et al., 2007). This increase occurs before the increase in plasma cortisol, which could explain the increased responsiveness of gill tissue to cortisol observed in early spring in coho and Atlantic salmon (McCormick et al., 1991) and also demonstrated *in vitro* in rainbow trout (Shrimpton and McCormick, 1999).

Interactions of Thyroid Hormones and Corticosteroids

Studies report interactions between HPT and HPI during smoltification. For example, TH can increase CRH neurogenesis during smoltification in Atlantic salmon (Ebbesson et al., 2011), suggesting a positive effect of TH on HPI. Cortisol treatment can lower plasma T_3 (but not plasma T_4) in coho salmon (Vijayan and Leatherland, 1989), during smoltification (Redding et al., 1991). The increases of *tr* mRNA and TR protein expressions and of plasma TH levels, observed during transfer from FW to SW, are lower in cortisol-injected smolt sockeye salmon compared to controls (Shin et al., 2014), suggesting some antagonistic/negative effects of cortisol on TH action.

Egg Hatching in Sauropsids

Thyroid hormones have an important role in fish egg hatching (tilapia: Reddy and Lam, 1991; Walpita et al., 2007; zebrafish: Heijlen et al., 2014; for review: Brown et al., 2014), but it will not be considered in this review, as egg hatching in fish implies less drastic changes of environmental conditions, as compared to sauropsids. In contrast, hatching in oviparous sauropsids, such as birds and reptiles, is characterized by a transition from a "protected" aqueous environment to a terrestrial environment exposed to desiccation and predation.

Egg Hatching in Birds

Involvement of Thyroid Hormones

Considering the implication of TH in egg hatching, one must differentiate precocial from altricial birds (McNabb, 2006; De Groef et al., 2013). Precocial species (e.g., chicken *Gallus domesticus*, Japanese quail *Coturnix japonica*, bobwhite

quail *Colinus virginianus*, turkey *Melleagris gallopavo,* mallard Pekin duck *Anas platyrhynchos*, goose *Anser anser*) have youngs that are immediately mobile and independent after hatching. In contrast, youngs of altricial birds (e.g., European starling *Sturnus vulgaris*, Ring dove *Streptopelia risorii*, red-winged blackbird *Agelaius phoeniceus*, great tit *Parus major*) need to be fed and thermoregulated by their parents in the nest (Starck and Ricklefs, 1998).

A gradual increase in plasma TH concentrations of the embryos to a peak is observed in precocial birds during the peri-hatch period (for review McNabb, 2006). In contrast, in altricial birds, circulating concentrations of TH are low during embryonic life and at hatching, and only increase after hatching (McNabb et al., 1984; Silverin and Rudas, 1996; Výboh et al., 1996; Olson et al., 1999).

Manipulation of egg TH levels influences avian hatching time. Injection of antithyroid drugs in the yolk sac of chick embryos retards hatching, and T_4 fully neutralizes these effects (Grossowicz, 1946; Adams and Bull, 1949; Romanoff and Laufer, 1956; Sinha et al., 1959; Balaban and Hill, 1971; Haba et al., 2011). In turkey, T_4 or T_3 injected to fertile eggs at Day 0 of incubation depresses hatchability, while improving it when administered at Day 25 of incubation out of a 28-day incubation period (Christensen, 1985). In Pekin duck, injection of T_3 results in earlier hatching, while injection of antithyroid drug delays hatching (Sirsat and Dzialowski, 2020). In Japanese quail, injection of T_4 alone or with T_3 doubles hatching success (Sarraude et al., 2020). Similarly, in a type 2 semi-altricial development model, the rock pigeon *Columba livia*, injection of a mixture of both T_3 and T_4 early results in higher hatching success but unchanged hatching time (Hsu et al., 2017).

In chicken, a differential temporal expression pattern of the three TR is observed. TRα mRNAs are detected as early as gastrula stage and throughout development in many embryonic tissues (Forrest et al., 1990). TRβ0 mRNAs appear later in embryonic life and are restricted to brain, eye, lung, and yolk sac (Forrest et al., 1990). TRβ2, a N-terminal variant of TRβ0, is predominantly expressed in retina (Sjöberg et al., 1992). The minimal generation of T3 until just before hatching is primarily due to the presence of DIO3 in chicken embryo liver (Galton and Hiebert, 1987). Hepatic DIO1 activity increases up to hatching and decreases thereafter, while hepatic DIO3 activity increases during embryogenesis, then decreases before hatching to remain low at post-hatching (Darras et al., 1992; Reyns et al., 2003). Dynamics of expression in deiodinases in the choroid plexus of the developing chicken brain have been reported: *dio1* and *dio2* mRNA levels increase over time to reach a peak around hatching, while *dio3* expression is high before hatching and decreases at hatching to re-increase up to 1 day post-hatching (Van Herck et al., 2015).

Involvement of Corticosteroids

An increase of avian embryonic GC is observed around the time of hatching in plasma (Wise and Frye, 1973; Kalliecharan and Hall, 1974; Siegel and Gould, 1976; Marie, 1981; Scott et al., 1981; Tanabe, 1982; Tanabe et al., 1983, 1986; Wentworth and Hussein, 1985; Porter et al., 2007), in adrenal glands (Tanabe et al., 1983, 1986), and in feces (Frigerio et al., 2001), and in adrenocortical cells in culture (Carsia et al., 1987).

Most studies investigating the effects of exogenous treatment of embryos with corticosterone in birds look at the postnatal growth and behavior linked to stress response (Rubolini et al., 2005; Saino et al., 2005; Freire et al., 2006; Hayward et al., 2006; Janczak et al., 2006; Henriksen et al., 2013; Zimmer et al., 2013; Weber et al., 2018). However, a few looked at the effects of GC treatment on hatching. Injection of corticosterone in the yolk sac 2 days prior to hatching shortens incubation time and increases hatchability in turkey (Wentworth and Hussein, 1985). In contrast, dipping fertile eggs in corticosterone prevents hatching in chicken (Mashaly, 1991). Elevation of plasma corticosterone levels by mean of synthetic GC (dexamethasone) injection during the final stages of incubation in chicken embryos increases or shortens incubation period when administered, on Day 16 and Day 18, respectively (Tona et al., 2007). In Japanese quail, incubation period is shortened in eggs laid by corticosterone-implanted hens (Schmidt et al., 2009). Chicken lung becomes sensitive to corticosterone prior hatching (Hylka and Doneen, 1983). Corticosterone treatment triggers prehatching stimulation of surfactant phospholipid synthesis (Hylka and Doneen, 1983). The first two studies reporting the cloning and developmental expression of pituitary GR in bird (chicken) gave different results: While Kwok et al. (2007) demonstrate constant expression of GR during embryonic period, other authors show an increase of GR mRNA levels (Porter et al., 2007).

Interactions Between Thyroid Hormones and Corticosteroids

Creating hypothyroidism in chick embryos induces a cortical atrophy and medulla hypertrophy in adrenal gland (Kingsbury et al., 1955). Injection of cortisol onto the allantoic membrane of 17 or 16-days old chicken embryos induces the same premature maturational changes in T_3 and T_4 metabolism observed naturally on 19–20-days old embryos, meaning a decrease of DIO3 preserving the T_3 formed, and an increase of DIO2 sparing T_4 (Borges et al., 1980). The administration of either dexamethasone or corticosterone, or ACTH to chicken embryos increase plasma T_3 concentrations and hepatic DIO2 activity (Decuypere et al., 1983) and increase plasma T_3 levels, decreased plasma T_4, decreased hepatic DIO3 activity and increased hepatic DIO1 activity (Darras et al., 1996).

Egg Hatching in Reptiles

Involvement of Thyroid Hormones

An increase in TH correlates with hatching in saltwater crocodile *Crocodylus porosus* (Shepherdley et al., 2002). In the grass snake *Natrix natrix*, the activity of the embryonic thyroid exhibits the features of a fully active gland at the time of hatching (Rupik, 2011). Injection of antithyroid drug into embryos of the snapping turtle *Chelydra serpentina* gives enlarged thyroid gland and delays hatching time (Dimond, 1954). Eggs of red-eared turtle, *Trachemys scripta*, treated with T_3, have shortened incubation duration (Sun et al., 2016). Embryos from Murray River short-necked turtle, *Emydura macquarii*, exposed to T_3, hatch earlier than untreated ones (McGlashan et al., 2017). Treatment of

saltwater crocodile embryos with T_3 increases DIO1 activity in liver and DIO2 in kidney (Shepherdley et al., 2002). Treatment with T_3 stimulates the secretion of phosphatidylcholine (PC, the major component of pulmonary surfactant) in sea turtle, *Chelonia mydas* (Sullivan et al., 2001). In saltwater crocodile, pre-treatment with T_3 increases surfactant phospholipids in lung (Sullivan et al., 2002a).

Involvement of Corticosteroids

An increase of corticosterone is observed from the last third of incubation to hatching in American alligator *Alligator mississippiensis* (Medler and Lance, 1998; Jennings et al., 2000). In contrast, a decrease in corticosterone is observed at hatching in saltwater crocodile (Shepherdley et al., 2002). Yolk corticosterone concentrations peak near the time of hatching in the tree lizard, *Urosaurus ornatus* (Jennings et al., 2000) and in sea turtles (Owens and Morris, 1985). In the tree lizard, treatment with corticosterone accelerates egg hatching (Weiss et al., 2007). Treatment with dexamethasone of saltwater crocodile embryos decreases DIO1 activity in kidney, DIO2 activity in liver and in kidney and DIO3 activity in liver (Shepherdley et al., 2002). Dexamethasone alone increases phospholipids from pulmonary surfactant in sea turtle when administered *in ovo* during late incubation (Sullivan et al., 2001). It also stimulates the secretion of phosphatidylcholine *in vitro* in saltwater crocodile (Sullivan et al., 2002a) and in lizard bearded dragon *Pogona vitticeps* (Sullivan et al., 2002b). In Chinese alligator *Alligator sinensis*, variations of the mRNA levels for *gr* in kidney, liver, and heart during embryonic development suggest a potential role for GC in tissue maturation before hatching (Izaz et al., 2021).

Interactions Between Thyroid Hormones and Corticosteroids

Treatment with dexamethasone and T_3 of saltwater crocodile embryos has effects on deiodinase activities: decrease of DIO1 activity in kidney, decrease of DIO2, and DIO3 activities in liver (Shepherdley et al., 2002). In the sea turtle *Chelonia mydas*, the secretion of phosphatidylcholine is stimulated by a combination of T_3 and dexamethasone before hatching (Sullivan et al., 2001). Similar results were obtained in the saltwater crocodile (Sullivan et al., 2002a) and in the lizard *Pogona vitticeps* (Sullivan et al., 2002b). All these data demonstrate the involvement of both TH and GC in the regulation of surfactant maturation in reptiles (Sullivan et al., 2003). Sullivan et al. (2003) reviewed the control of pulmonary surfactant and stated that dexamethasone and T_3 are crucial stimulators of surfactant production during embryonic development throughout evolution.

Birth in Mammals

Involvement of Thyroid Hormones

During most of the gestation in human, T_4 is converted in rT_3, while toward term, developmental changes in tissue deiodinase activity occur, leading to preferential deiodination of T4 to T3 (instead of rT_3) and rise in plasma T_3 concentration near term (Forhead and Fowden, 2014). In contrast, in the rat, circulating T_3 concentrations do not increase before birth (Dubois and Dussault, 1977; Harris et al., 1978; Lamers et al., 1986). Comparison of hormonal profiles during the perinatal period in two closely related murine species with distinct modes of development (altricial vs. precocial), the rat (altricial), and the spiny mouse *Acomys cahirinus* (precocial) allowed to show a correlation between perinatal increase in T_3 levels and precocial timing of birth (Lamers et al., 1986).

TH have a major regulatory role on fetal growth (Forhead and Fowden, 2014), and maturation of the central nervous system (Patel et al., 2011; Stenzel and Huttner, 2013). Furthermore, maternal hypothyroidism is associated with increased rates of respiratory distress syndrome in new-born (Casey et al., 2005; Männistö et al., 2013) and cardiorespiratory disorder (Rousseau et al., 2019). In various mammalian species, TH change the synthesis of the components of surfactant (Ballard et al., 1984; Das et al., 1984; Warburton et al., 1988; Gilbert et al., 2001; Van Tuyl et al., 2004). TH are also involved in the intestinal structural development (Trahair and Sangild, 1997; Sirakov and Plateroti, 2011; Sirakov et al., 2014). Specific TRα1 loss-of-function leads to low development and impaired activity of murine intestinal stem cells in culture (Godart et al., 2021). In addition, *in vivo* treatment confirms the positive action of T_3 on intestinal crypt cell proliferation and demonstrates its key action in modulating the number of stem cells, the expression of their specific markers and the commitment of progenitors into lineage-specific differentiation (Godart et al., 2021).

Involvement of Corticosteroids

An increase of plasma fetal GC is detected near parturition in many mammals (Alexander et al., 1968; Mulay et al., 1973; Lamers et al., 1986; Silver and Fowden, 1989; Yoon et al., 1998). The involvement of HPA axis in the timing of birth is first evidenced in ovines (Van Rensburg, 1967; Barnes et al., 1977). Furthermore, premature delivery is induced by injection of ACTH or corticosteroids into the ovine fetus (Van Rensburg, 1967; Halliday and Buttle, 1968; Liggins, 1968, 1969) as well as in fetal piglet (Bosc, 1973). More recently, the use of antalarmin, a CRH-R type I antagonist, can delay the onset of parturition in sheep, which suggests that CRH is involved in the induction of parturition in this species (Chan et al., 1998).

The many roles of GC on organ maturation have been the subjects of recent reviews (Fowden and Forhead, 2015; Fowden et al., 2016; Jellyman et al., 2020). As for TH, we will concentrate on GC involvement in lung and gastro-intestinal tract (GIT) maturations, which are crucial to cope with the change of environment (from aquatic to terrestrial) and of nutrition (from parenteral to enteral), respectively. In lambs born prematurely by infusion of dexamethasone, partial aeration of the lungs is noted, suggesting an accelerated appearance of surfactant activity (Liggins, 1969). Infusion of ACTH into one of twin pairs of lamb fetuses accelerates the morphological changes, that would normally occur in the lung, before birth (Sundell et al., 1979). GC treatment changes the synthesis of the phospholipid and protein components of surfactant (Warburton et al., 1988; Gilbert et al., 2001). At birth, there is a shift from mainly parenteral nutrition in the fetus (via the placenta) to enteral nutrition in the neonate, and the GIT has to prepare during gestation for coping with this change. This prenatal development of GIT is regulated by GC (Trahair and Sangild, 1997; Sangild et al., 2000). After bilateral

adrenalectomy of fetal sheep, growth of mucosal structures and villus height are reduced in the small intestine (Trahair et al., 1987a). After infusion of cortisol, no change in enterocyte morphology is detected, but the proportion of crypt cells and the migration of enterocytes are increased (Trahair et al., 1987b). In addition, cortisol influences the prenatal development of gastric acid and gastrin secretion, and of GIT hydrolase activities in both the fetal pig and sheep (Trahair and Sangild, 1997; Sangild et al., 2000).

Interactions Between Thyroid Hormones and Corticosteroids

Before birth, TH and GC synergize for the maturation of various organs, especially the lung, the liver and the brain. This synergism is partly linked to the fact that GC induce local deiodinase expression and activities resulting in the increase of circulating T_3 and thus T_3 bioavailability (Forhead et al., 2006; Fowden and Forhead, 2009). A synergism of TRH/T_3 and cortisol has been reported on lung maturation in fetal sheep, as infusion of cortisol and TRH (Liggins et al., 1988) or T_3 (Schellenberg et al., 1988; Warburton et al., 1988) increase the distensibility and the stability of the lung. In explant culture of human fetal lung, a supra-additive response in the synthesis of surfactant is observed in the presence of both dexamethasone and T_3 (Gonzalez et al., 1986).

T_4 injection to rats induces a precocious appearance of pepsinogen in the oxyntic gland mucosa and increases acid secretion, while in propylthiouracil-induced hypothyroid pups, pepsinogen content and basal acid secretion are low (Tseng and Johnson, 1986). However, T_4 has no such effects in adrenalectomized rats, while corticosterone is able to increase pepsinogen content and basal acid secretion in the absence of normal levels of TH (Tseng and Johnson, 1986).

Comparison of the Involvement and the Interdependence Between Thyroid and Corticosteroid Signaling in Vertebrate Developmental Transitions

In all the major developmental transitions described here, a common synergistic activation of thyrotropic and corticotropic axes is observed, leading to synchronized increase of TH and CS production and release (**Figure 4**). Besides this hormonal activation, increased expression of receptors allows tissues to become more responsive to TH and CS in time (**Figure 4**) to induce morphological, behavioral and physiological changes when needed, meaning just before the animal has to adapt to its new environment and its new way of life. As in all the mechanisms underlying major biological processes, they are conserved along evolution. Thus, the involvement of both TH and CS signaling is encountered in fish and amphibian metamorphic processes, as well as in egg hatching in sauropsids and birth in mammals (**Table 1**).

In non-mammalian vertebrates, the neurohormone, corticotropin-releasing hormone (CRH), appears to be potentially a coordinator of activation of both thyrotropic and corticotropic axes, as it is able to simulate thyrotropin production and release as much as corticotropin ones. CRH may thus be involved in the simultaneous activation of these neuroendocrine axes at the time of developmental transitions in non-mammalian vertebrates, such as fish and amphibian metamorphoses or sauropsid egg hatching (**Table 1**). It is not the case in mammals, in which the thyrotropic and corticotropic axes are controlled centrally by different hormones, respectively, TRH and CRH. Another difference among vertebrate developmental transitions described in this review may lay in the degree of involvement (triggering vs. permissive) of the two signaling systems and their interdependence. Except perhaps during birth for mammals, corticosteroid signaling seems to be more permissive than crucial, in the way it allows the thyroid signaling to be even more efficient, by elevating the activating deiodinase expression and activities, as well as the expression of TH receptors. Another difference may be likely due to neofunctionalization of gene paralogs observed after WGD. Duplication of some genes, notably in teleosts, may lead to redistribution of function. For example, the involvement of *tshβ1b* at smoltification in Atlantic salmon, instead of the classical *tshβ* in other vertebrate developmental transitions, or also the relative importance and differential role of the various thyroid hormone receptors between flatfish and amphibian larval metamorphoses.

IMPACT OF ENVIRONMENTAL FACTORS ON POST-EMBRYONIC TRANSITIONS

Climate Change

Water Warming for Population Strictly Dependent on an Aquatic Habitat

Teleost fish as ectothermic vertebrates show complex responses to temperature variation (Pinsky et al., 2019). Temperature has in teleost fishes a direct effect on oxygen delivery, cardiovascular function, muscle function, food conversion, mitochondria efficiency, and biochemical reaction rates (Little et al., 2020). Fish physiology is thus likely to be affected by increases in average temperature and temperature variability leading to energy metabolism changes with impact on growth and locomotion. All these physiological processes have been associated with thyroid function.

T_3 regulates thermal acclimation in zebrafish (Little et al., 2013) with the decrease of metabolism, skeletal muscle function and swimming performance in hypothyroid cold-acclimated (18°C) but not hypothyroid warm-acclimated (28°C) animals. The interactions between temperature levels, thyroid conditions and swimming performance are also linked to performance of the heart and oxygen transport (Little and Seebacher, 2014). In the context of global warming, the low sensitivity to TH at warm temperature is a concern because it may reduce the capacity of zebrafish to match this environmental change. Furthermore, in medaka, exposure until hatching to warm temperatures (32°C) increases the activation of TH biosynthesis, via TSH (Castañeda-Cortés et al., 2020), as well as the activation of the stress axis, via CRH (Castañeda-Cortés et al., 2019).

Rainbow trout is a typical cold-water fish species for which seasonally warmer water correlates with a decrease in fry survival

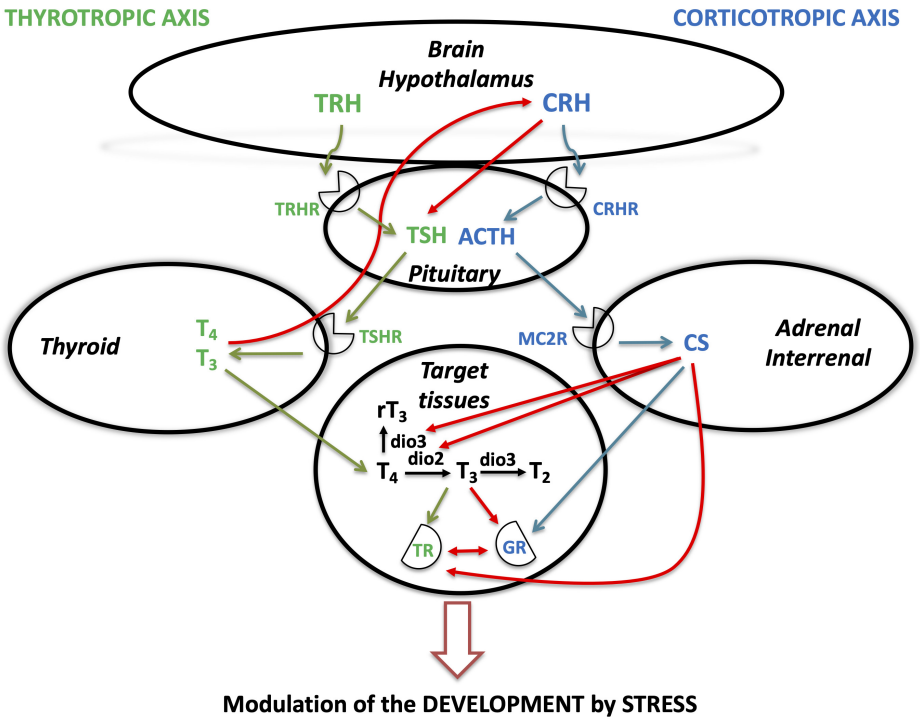

FIGURE 4 | Interactions between thyrotropic and corticotropic axes during vertebrate developmental transitions. The figure illustrates current knowledge on the interactions between the thyrotropic (HPT) and corticotropic (HPA/HPI) axes, during various developmental transitions (amphibian and teleost metamorphoses, sauropsid egg hatching and mammalian birth). ACTH, adrenocorticotropin; CRH, corticotropin-releasing hormone; CRHR, corticotropin-releasing hormone receptor; CS, corticosteroids; dio, deiodinase; GR, glucocorticoid receptor; MC2R, melanocortin receptor 2; MR, mineralocorticoid receptor; T_4, thyroxine; T_3, triiodothyronine; rT_3, reverse triiodothyronine; T_2, diiodothyronine; TR, thyroid hormone receptor; TRH, thyrotropin releasing hormone; TRHR, thyrotropin releasing hormone receptor; TSH, thyrotropin; TSHR, thyrotropin receptor.

TABLE 1 | Comparison of the interactions between HPT and HPA axes during vertebrate developmental transitions.

	Vertebrates	Amphibian	Teleost	Sauropsid	Mammal
	Developmental period	**Metamorphosis**	**Metamorphosis**	**Egg hatching**	**Birth**
HPT axis on HPA/I axis	TH on CRH	+	+	+	+
	TH on CS availability	?	?	?	+
	TH on GR	+	+	+	+
HPA/I axis on HPT axis	CRH on TSH	+	+	+	-
	CS on TH availability	+	+	+	+
	CS on TR	+	+	+	+

and an increase of T_3 and T_4 concentrations (Giroux and Schlenk, 2021). Transcriptome analysis of liver tissues from adult rainbow trout under heat stress (24°C) and control conditions (18°C) identifies the differential expression of 428 long non coding RNA some of which can be involved in maintenance of homeostasis or adaptation to stress (Quan et al., 2020). In Atlantic salmon, elevated temperature increases T_4 nocturnal levels (Nisenbaum et al., 2020). Thus, future climate changes can induce lower salinity tolerance and accordingly result in poor survival in seawater after smoltification.

To show the wide diversity of the links between global warming and TH, we will give three more examples. First, in the mosquitofish *Gambusia holbrooki* the thermal acclimation is mediated by TH and leads to decreased mitochondrial efficiency, metabolic rates, and swimming performance (Le Roy and Seebacher, 2020). Second, in the desert fish Amargosa pupfish *Cyprinodon nevadensis amargosae*, temperature contributes to altered TH levels and morphological development (Lema et al., 2016). We can thus expect that many desert fishes will be vulnerable to rising temperatures because they occupy habitats with already high temperatures. Finally, increased temperature induces a decrease of TH levels in convict surgeonfish *Acanthurus triostegus* (Besson et al., 2020). The effect on TH levels correlates with affected sensory development leading to higher predation.

Chronic temperature increases (persisting for a long time) are also known to induce acute stress responses in fishes

(Alfonso et al., 2020). Global warming can cause water freshening from increased freshwater inputs. In Antarctic spiny plunderfish *Harpagifer antarcticus*, salinities decrease leads to high plasma cortisol levels compare to normal salinity (Vargas-Chacoff et al., 2021). This has implications for fish species that have evolved in stable environmental conditions like in the Antarctic. In a totally different environment, climate-induced bleaching of coral reefs alters anemonefish hormonal stress, resulting in decreased reproductive hormones and severely impacted reproduction (Beldade et al., 2017). Finally, in juvenile brown trout, *Salmo trutta*, water temperature affects cortisol and GR mRNA levels (Filipsson et al., 2020).

Aquatic and Terrestrial Life Cycle: Warming Leads to Double Penalty

Amphibians are another ectodermic taxon with complex interactions between costs and benefits of life in the aquatic and terrestrial environments. They are undergoing a precipitous decline linked with environmental pressures including climate change. Many amphibian species exploit temporary or even ephemeral aquatic habitats for reproduction. Survival from desiccation of pond drying is reached by maximizing larval growth and acceleration of development, including precocious metamorphosis.

The western spadefoot toad tadpoles, *Pelobates cultripes*, usually have long larval period, but it can shorten it in response to pond drying (Gomez-Mestre et al., 2013). Developmental acceleration correlates with increased corticosterone and TH levels as well as increased TRβ levels to increase metamorphic process. Anuran tadpole shows thus phenotypic plasticity in age and size at metamorphosis as a response to temperature variation (Ruthsatz et al., 2020). In Arizona tiger salamander *Ambystoma tigrinum*, the small increase in temperature tends also to decrease the time to metamorphosis and results in a worse body condition (Park et al., 2016). Plasticity in rates of growth and development is beneficial to allow a more rapid transition into the juvenile stage where rates of mortality are lower. However, early metamorphosis leads to juveniles with smaller size correlated with low survival and locomotor performance (Székely et al., 2020). Pond drying may also lead to the loss of the capacity to respond to desiccation following decreased food availability (Enriquez-Urzelai et al., 2013), liver damage with upregulation of DIO2 and TRα transcript levels while there is a decrease of TRβ (Chen et al., 2021), or increased oxidative damage during metamorphosis (Petrović et al., 2021).

TH and GC level variations underlie differences in the timing of metamorphosis. In response to pond drying, western spadefoot toad and New Mexico spadefoot toad *Spea multiplicata* that have long larval periods and large size at metamorphosis, accelerate metamorphosis and elevate whole-body content of TH and corticosterone (Kulkarni et al., 2017). In contrast, in Couch's spadefoot toad *Scaphiopus couchii* that has a short larval period, whole-body TH and corticosterone content are high during metamorphosis and weakly affected by pond drying. Thus, species exhibiting less plasticity will be more sensitive to environmental changes. The TH and CS level variations to accelerate metamorphosis during habitat desiccation may originate from elevated CRH (Denver, 1997). CRH can be a transducer of environmental stimuli to modulate the rate of metamorphosis *via* the endocrine response. Interestingly, CRH has also been shown to control the term of pregnancy in mammals. Maternal plasma CRH concentrations are elevated early in pregnancy in those patients destined to deliver preterm, and are lower in patients destined to deliver post-dates (Challis and Hooper, 1989; McLean et al., 1995).

Climate Changes and Terrestrial Biodiversity

Temperature increase alters avian phenotypes such as advanced reproduction, migration schedules and individual appearance. Bird ability to maintain a stable body temperature in a wide range of thermal environments is regulated *via* endocrine pathways including TH and with a lesser extent CS (Ruuskanen et al., 2021). The knowledge on endocrine regulation of thermogenesis concerns mainly poultry, but poorly describe for environmental temperature variation. Offspring development are dependent of females via hormones deposited in eggs. Ambient temperature changes affect the hormone levels in the yolk including TH and CS. More specifically, T_4 levels were negatively correlated with ambient temperature in great tits *Parus major* (Ruuskanen et al., 2016). However, in wild pied flycatchers *Ficedula hypoleuca*, there is no evidence for context-dependent effects of prenatal TH related to postnatal temperature on growth, survival, and plasma TH levels (Hsu et al., 2020), suggesting species differences or unknown confounding effects.

In reptiles and turtles, temperature effect on TH and GC plasma levels is controversial being either absent, positive or negative. Highlighting only a few examples, in the alligator lizards *Elgaria coerulea* and *Elgaria multicarinata*, corticosterone levels increase with temperature (Telemeco and Addis, 2014) and in the South-American tegu lizard *Salvator merianae*, T_3, T_4, and corticosterone levels show a positive relationship with body temperature (Zena et al., 2020). Similar correlation between body temperature and plasma corticosterone is observed in the eastern fence lizards *Sceloporus undulatus*, under laboratory conditions, but not in the field (Racic et al., 2020). In contrast, in the common lizard *Zootoca vivipara*, baseline corticosterone levels decrease with increasing thermal conditions (Dupoué et al., 2018).

In mammals, we will only highlight two of the numerous examples. First, the transition between late gestation and early lactation is a developmental window sensitive to warming. Dairy cows experience stress due to the high energy and nutrient requirements of the fetus and the mammary gland. In early lactation, the decline of TH levels is more pronounced in cow maintained at 28°C compared to the one maintained at 15°C (Weitzel et al., 2017). The second example is an Artic mammal, which has highly evolved to these extreme environments and its capacity to adapt to this change may be limited. The polar bear is emblematic to this environment. It was shown that CS binding capacity of plasma CS binding globulin increases in polar bears as a consequence of climate warming (Boonstra et al., 2020). Evidence is still lacking to have a complete view of the interactions between GC and TH in response to global warming.

Endocrine Disruptors

Thyroid Function Disruption

As previously mentioned, TH orchestrates metamorphosis, brain development, and metabolism representing a potential target for endocrine disruptor chemicals/compounds (EDC). Although the molecular mechanisms for TH disruption is still unknown for most of the EDC, several affect TH synthesis, transport or metabolism and downstream effects (Thambirajah et al., 2019). One of the main concerns is disruption during early neurogenesis, which may affect several TH actions such as proliferation, differentiation, migration, synaptogenesis and myelination in the developing nervous system (Préau et al., 2015).

Because anuran metamorphosis is strictly dependent on TH, amphibians represent sensitive models for the detection and mechanistic elucidation of TH disrupting activities (thyroid histology, metamorphosis progression). EDC impact wild anurans and contribute to population declines. Some pesticides and biocides may interfere with TH signaling during nervous system development (Leemans et al., 2019; Trudeau et al., 2020) or metamorphosis timing (Orton and Tyler, 2015). Last but not least, exposition of *Xenopus* tadpoles to the benzo[a]pyrene leads to delayed metamorphosis and sexual maturity with transgenerational disruption of metabolism and population decline (Usal et al., 2021).

In zebrafish, exposure during the 7 first days of development to 25 known TH disrupting compounds leads to morphological defects and variations of transcripts involved in the HPT axis (Spaan et al., 2019). In another teleost fish, the metamorphosing convict surgeonfish *Acanthurus triostegus*, high doses of the pesticide chlorpyrifos induce defects by decreasing TH levels impacting olfactory, visual and mechano-sensory structure development (Besson et al., 2020). Interestingly, similar phenotypes were observed following temperature increase, highlighting the profound threat anthropogenic stressors pose to fish communities. To highlight the EDC mode of action, liver transcriptomic responses in yellow perch *Perca flavescens* population show variation of genes transcripts related to reproduction, retinol, iron, TH, oxidative stress, lipid metabolism, and immune functions between strongly impacted population vs. less impacted groups (Defo et al., 2018).

In birds as in teleost fishes and amphibians, because GC regulate metabolism, ability to modulate corticosterone in response to stressor is essential to face a wide array of environmental challenges. EDC contamination was shown to impair this GC role. Methylmercury exposure reduces stress-induced GC response in zebra finches, *Taeniogypia guttata* (Moore et al., 2014). TH function is also EDC target. The rural nestling peregrine falcon *Falco peregrinus* has significantly lower circulating concentrations of TH compared to urban nestlings where flame retardants are environmental contaminants that accumulate in predatory birds (Fernie et al., 2017).

EDC also affect TH signaling in mammals. Considering the large amount of recent data available, only a few examples will be given here. In mice, exposure to the flame-retardant, tetrabromo bisphenol A, modulates hypothalamic set-points controlling metabolic responses by targeting TR regulation of *trh* and *mc4r* (Decherf et al., 2010). In the polar bear *Ursus maritimus*, an heavily polluted organism for which some EDC are banned for decades (Routti et al., 2019), some EDC, such as organochlorine and perfluoroalkyl, are negatively correlated with plasma TH levels (Bourgeon et al., 2017). In wild chimpanzees, contamination by polluted drinking waters containing pesticides (Krief et al., 2017) and bisphenols (Krief et al., 2020) has been reported, and the water samples exhibit TH disrupting activities (Spirhanzlova et al., 2019). Experimental exposure of *Xenopus laevis* tadpoles to a mixture of 15 chemicals at concentrations reported in human amniotic fluid induces variation of behavior, of TH-responsive gene expression and of nervous system development (Fini et al., 2017). Considering the conservation of TH function across vertebrates, one may speculate on such impacts of amniotic fluid chemicals on human fetal brain development.

Environmental and health concerns remain particularly challenging when addressing thyroid hormone axis disruption. Only few chemicals have been tested, the number of test methods is limited and the thyroid system is complex. The development of specific chemical safety testing is required (Browne et al., 2020) with special attention to neurological development (Gilbert et al., 2020; Kortenkamp et al., 2020; O'Shaughnessy and Gilbert, 2020). Attention is also paid to break down the wall between mammalian and non-mammalian vertebrate regulatory testing (Couderq et al., 2020; Holbech et al., 2020). In addition to phenotypic or histological end-points, the use of molecular assays (transcripts, proteins or metabolites) will be more sensitive and most of all will allow detection before adverse effects occur (Fini et al., 2007; Kulkarni and Buchholz, 2013). Development of non-destructive (without euthanasia) biomarkers that provide causal link between the presence of a chemical and an ecological effect are also needed to allow the study of vulnerable populations.

Corticosteroid Function Disruption

The adrenal has been neglected in endocrine disruption regulatory testing strategy while the negative consequences of adrenocortical dysfunction during development have been recognized (Hinson and Raven, 2006; Harvey, 2016). Upstream of the biological effect, an activity mimicking that of GC was measured in surface waters (Schriks et al., 2013). Hydrocortisone was detected but could not explain a significant fraction of the observed GR activity.

GC synthesis pathway is also a target. Different environmental toxicants, including phthalate esters together with bisphenols and their analogs pose deleterious effects on the biosynthesis of GC *in vitro* (Ahmad et al., 2017; Verma et al., 2018). These observations were confirmed *in vivo* using nitrate, a major anthropogenic contaminant in the FW environment. In three-spined stickleback *Gasterosteus aculeatus* L., dissolved inorganic N directly exerts a disruptive influence on the function of the stress axis and GC levels, supporting concerns that nitrate is an EDC (Pottinger, 2017). GC disruption was linked to adverse effect in zebrafish exposed to methylparaben, widely used as antimicrobial preservative. In addition to increase in

cortisol levels, animals show alteration of heart rate and hatching percentage as well as signs of anxiety-like behavior (Luzeena Raja et al., 2019).

Finally, because persistent organic pollutants can interact with GR, EDC mixtures were screened for GR translocation and GR transactivation in an *in vitro* assay (Wilson et al., 2016). EDC mixtures did not induce GR translocation in nucleus nor produce an agonist response in the GR transcriptional assay. However, in the presence of cortisol, some chemicals were found to decrease GR transcriptional activity.

Endocrine Disruptor Chemicals/Compounds and Climate Change: A Worst Combination

Climate change and exposure to EDCs are currently two of the most serious anthropogenic threats to biodiversity and ecosystems. Moreover, the ecological threats posed by EDC are further exacerbated by changing environmental conditions such as temperature, pond drying, food restriction, pH and ultraviolet radiation.

In aquatic environment, global warming may lead to temperature increase associated with either salinity increase due to evaporation or salinity decrease due to ice melting. One study addresses the combinatorial effect of temperature, salinity and diuron, an herbicide and antifouling agent with EDC property (Moreira et al., 2018). Combinatorial treatment of juveniles of the estuarine fish, the inland silverside *Menidia beryllina*, affects growth and hormonal levels. T_3 increases in all of them, while T_4 increases at low temperature and low salinity and decreases at low temperature and high salinity, in agreement with DIO2 expression. EDC, acidification and other contaminants can also perturb smolt development, resulting in poor survival after salinity increase (Björnsson et al., 2011). In the San Francisco Bay, the rainbow trout experiences warmer waters and saltwater intrusion (Giroux and Schlenk, 2021) leading to fry decrease in survival associated with TH increase. Our last example in teleost fishes highlights the interaction between temperature and perchlorate, a well-known thyroid disruptor (Lee et al., 2014). Overall, the results suggest that perchlorate affects thyroid function and reproduction, and these adverse effects are worsened under high temperature.

As previously described in amphibians, a rapid transition into the juvenile stage is beneficial in stress conditions. Pond desiccation is associated to a decrease in dissolved oxygen and an increase in nitrogen levels for which anthropogenic sources such as chemical fertilizers can be heavily suspected. Ammonium nitrate or hypoxic conditions leads to survival decrease of the Natterjack toad *Bufo calamita* tadpoles (Ortiz-Santaliestra and Marco, 2015). When both stressors were combined, the lethal effects were additive and include malformations. Global warming lead also to predator-prey relationship modifications decreasing survival rates of tadpoles (Jara et al., 2019). In addition, the Bullfrog sensitivity to temperature leads to corticosterone hormonal changes that correlate with immunosuppression (Lima et al., 2020) and increases sensitivity to emerging infectious diseases in the concept of OneHealth. Urodela amphibians are also affected. Compared to a single exposure, Arizona tiger salamander larvae subjected to both temperature increase and perchlorate treatment further decrease their rate of development. These cotreated salamander larvae also present a significant smaller body mass and worse body condition.

Finally, Artic biodiversity is concerned by this double threat. EDC were measured in Arctic marine mammals and seabirds. The most pronounced relationships with endocrine function have been reported with the thyroid hormone system, the sex steroid hormones and cortisol (Jenssen, 2006). Because these endocrine systems are essential for completing life cycles and enabling animals to respond adequately to environmental stress, EDC may interfere with adaptations to increased stress situations.

CONCLUSION

We have highlighted the roles of TH- and CS-regulated developmental transitions in the innovation, adaptation and plasticity of life cycles in vertebrates. In one of his review, Buchholz discusses the similarities between birth in mammals and metamorphosis in frog with a focus on their regulation by TH and GC (Buchholz, 2015). He reminds us that "both frogs and mammals undergo a life history transition from aquatic (water and amniotic fluid) to terrestrial habitat," involving for the most striking examples, air-breathing thanks to lung maturation and maturation of the intestine to cope with the transition to a new food source. Similar TH and CS concentration profiles are observed in certain birds and reptiles at hatching and during molting, as well as in certain teleost fishes at hatching and during larval metamorphosis and smoltification (Wada, 2008). The multiple cross-talks between HPT and HPA/HPI axes represent critical mechanisms by which vertebrates modulate their perinatal/post-embryonic development as well as their responses to a changing environment (**Figure 4**).

The exposome includes stressors with, for some, potential mortality risk by their long-term effects. Vertebrate respond to the risk/benefit trade-off by modulating the production of hormones by the stress and thyroid neuroendocrine axes. In this context, global warming leads to increases in average temperature and temperature variability. Considered as a threat for biodiversity (Radchuk et al., 2019), global warming is a well-known reprotoxicity risk (Parisi and Guerriero, 2019). However, the properties of TH and CS suggest their fundamental roles in thermal acclimation (de Bruijn and Romero, 2018), and evolution of ectothermy/endothermy (Little, 2021). Changes in hormone sensitivity at warm temperatures could mean that increasing temperatures will reduce the capacity of animals to regulate their physiologies to match demands. Aquatic and terrestrial environments are also increasingly contaminated by anthropogenic sources. The contaminants include pharmaceuticals, personal care products, and industrial and agricultural chemicals. Many of these chemicals have the potential to disrupt endocrine function that may lead to disease or

foundations to disease later in life as well as disease transmission to descendants (Gore et al., 2015). The adverse effects including metabolic diseases, decreased capacity of reproduction, hormone-sensitive cancers, thyroid disorders, and neurological defects may contribute to population decline. The difficulties tie in the circumstances EDC act, including non-monotonic dose-responses, low-dose effects, and developmental vulnerability. Possible roles for the neuroendocrine stress axis in mediating these developmental responses requires further investigation.

AUTHOR CONTRIBUTIONS

All Authors contribute equally to the redaction of the review.

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