REVIEW PAPER

Early environment influences later performance in fishes

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Conditions fish encounter during embryogenesis and early life history can leave lasting effects not only on morphology, but also on growth rate, life-history and behavioural traits. The ecology of off-spring can be affected by conditions experienced by their parents and mother in particular. This review summarizes such early impacts and their ecological influences for a variety of teleost species, but with special reference to salmonids. Growth and adult body size, sex ratio, egg size, lifespan and tendency to migrate can all be affected by early influences. Mechanisms behind such phenotypically plastic impacts are not well known, but epigenetic change appears to be one central mechanism. The thermal regime during development and incubation is particularly important, but also early food consumption and intraspecific density can all be responsible for later life-history variation. For behavioural traits, early experiences with effects on brain, sensory development and cognition appear essential. This may also influence boldness and other social behaviours such as mate choice. At the end of the review, several issues and questions for future studies are given.

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Key words: epigenetic effects; growth; life-history traits; maternal effects; sex ratio; social behaviour.

INTRODUCTION

Animal traits are influenced by early life experiences. For almost a century, research has revealed how environments of embryos influence skeleton and muscle development of ectothermic animals including fishes (Tåning, 1952; Lindsey, 1988; Wimberger, 1992; Johnston, 2006; Sfakianakis *et al.*, 2011). Less is known about how early influences can change sex differentiation, later growth rate, life-history traits and behaviour of organisms. These issues did not receive much attention before the theory on life-history evolution and flexibility was developed in the latter part of the 20th century (Roff, 1992; Stearns, 1992). Most empirical knowledge on these effects is therefore recent (Danchin & Wagner, 2010; Salvanes *et al.*, 2013).

Phenotypes emerge from complex interactions between genes and environment (Gilbert & Epel, 2008), and development effects are caused by conditions that organisms experience during embryogenesis (Martin *et al.*, 2013). The earlier the environmental disturbance, the stronger its long-term effects can be (Lindström, 1999). Developmental effects are often overlooked when studying life-history variation, and

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phenotypic variation in characteristics, such as growth rate, age at maturity and repro-
ductive investments, can easily be misinterpreted for genetic differentiation. Thus,
possible effects of early influences should be considered when studying ecological
variation along environmental gradients or between contrasting environments.

A growing body of literature suggests that phenotypic plasticity caused by early
experience play a critical role in brain development and flexibility influencing cog-
nition, behaviour, social skills, stress responsiveness and personality development
(Malekpour, 2007; Gudsnuk & Champagne, 2011). Also, however, life-history traits,
growth and age at developmental shifts are phenotypically plastic and can be affected
by early stimuli (Schlichting & Pigliucci, 1998; Jonsson & Jonsson, 2011). For
example, poor environmental conditions early in life can give low growth, small adult
size and small energy reserves (Taborsky, 2006). Together, such changes reduce the
competitive ability of organisms with subsequent negative effects on reproductive
success and fitness (Arendt, 2000; Lummaa & Clutton-Brock, 2002). Hence, devel-
opmental effects can have paramount importance for understanding life-history and
behavioural variation in animal populations. In this review, examples from teleosts
and salmonids in particular will be presented. These will illustrate how early envi-
ronments can influence growth, sex differentiation, life histories and behavioural
performances.

The mechanisms behind developmental variation are more abstruse. It is known
that environmentally induced change in metabolic rate and growth rate with asso-
ciated life-history effects can be influenced by thermal and nutritional conditions
(Elliott, 1994). Furthermore, the regulation can involve modifications of the epigeno-
type (Gilbert, 2005; Cabej, 2012) initiating neural, hormonal and enzymatic effects
(Gabillard *et al.*, 2005; Rungruangsak-Torrisen *et al.*, 2006; Crews, 2010; Nelson &
Monteggia, 2011). It is also known that there are limits for phenotypically plastic
variations and that these limits can be inherited (Scheiner & Holt, 2012; Mesoudi
et al., 2013). Physiologically, gene expressions can be altered through a neuroen-
docrine pathway: the nervous system monitors the environment and transfers signals
to the endocrine system. The endocrine hormones can then alter gene expression.
Alternatively, gene expressions can be changed as an epigenetic effect not altering
the underlying DNA sequence. This may be caused by a change in the environmen-
tally induced methylation pattern of the genome, which can alter its transcriptional
capabilities. Although epigenetic [epi = over or above (the genetics)] variations are
independent of the nucleotide sequence, they can still be inherited over generations
(Bossdorf *et al.*, 2008). Other epigenetic mechanisms may be involved, that are
mentioned later in this review. There are many uncertainties concerning epigenetic
mechanisms influencing phenotypic flexibility, and information on fishes is chiefly
restricted to studies of model species such as zebrafish *Danio rerio* (Hamilton 1822),
and medaka *Oryzias latipes* (Temminck & Schlegel 1846) (Iida *et al.*, 2006; Mirbahai
et al., 2011).

This review focuses on how early experiences can affect development and later per-
formance in fishes, *i.e.* how they accomplish given tasks against known standards. The
review is mainly limited to influences prior to external feeding, but in a few cases it
also includes social influences during the first period of external feeding. Later effects
include phenotypic effects visible during later juvenile and adult stages. Characteristics
included are juvenile growth and adult body size, sex determination, life-history char-
acteristics such as age at maturity, egg size and fecundity, partial migration, survival

and lifespan. Behavioural aspects covered are social behaviour towards conspecifics, risk taking, anti-predator behaviour, cognition and mate choice.

The presentation commences by limiting the field reviewed. Then, mechanisms by which early influences can be conveyed are presented. The thermal environment is most important in the review of growth, sex determination and life-history effects. Effects of social environments have received most attention in studies of behavioural aspects. Salmonids dominate the examples illustrating life-history effects of early influences, whereas model species are more important in the behavioural aspects covered. At the end of the review, several issues and questions for future studies are suggested.

The review does not penetrate deeply into the molecular or physiological basis for such effects, but mentions theories on how the environment may influence functional phenotypes. The review does not cover anomalies caused by overexposure to temperature, heavy metals or other toxic substances. Environments' effects upon genes are central in oncological research and can influence the initiation and development of cancers (Chik *et al.*, 2011; Dawson & Kouzarides, 2012), but these effects are also outside the scope of this paper.

EARLY EXPERIENCES WITH EFFECTS ON LATER PERFORMANCE AND LIFE HISTORY

WHAT IT IS

Eggs, embryos, larvae and young juveniles can encounter environments with significant effects on their subsequent morphology, physiology, behaviour and life history. For instance, the thermal environment does not only influence the development of specific organs, muscles or other body parts of the embryo, but can also influence ecological traits such as individual growth rate, age and size at ontogenetic niche shifts, age at maturity, fecundity, egg size and lifespan (Table I). All these characteristics can affect subsequent reproductive success and fitness (Harrison *et al.*, 2010).

Developmental effects can be caused by favourable conditions during embryogenesis, which exert positive long-term influences in adult life ('silver spoon effects'). Favourable temperature conditions during the egg development can increase developmental rates and give organisms head starts relative to those developed under less favourable conditions. Advanced developmental rate can reduce age and size at ontogenetic niche shifts with possible consequences for survival and reproductive success (Jonsson, *et al.*, 1990*a, b*, 2005; Madsen & Shine, 2000). Such effects are observed in fishes (Koumoundouros *et al.*, 2009), but more studied in reptiles (Warner *et al.*, 2010) and mammals (Descamps *et al.*, 2008).

Behavioural patterns can be based on early experiences and be permanently retained. For instance, male first-generation sea-ranched Atlantic salmon *Salmo salar* L. 1758 are bolder and exhibit prolonged, intraspecific combats compared with wild conspecifics from the same population (Fleming *et al.*, 1996, 1997). Wild *S. salar* grow up in natural rivers where they meet larger and stronger fish, and it can pay to be careful and hide or exhibit subordinate postures and colouration when meeting superior competitors (Hollis *et al.*, 2004; Stuart-Fox & Moussalli, 2008). In contest competition, *S. salar* in rivers perform rapid attacks and retreats and thereby avoid being injured by stronger fish. Sea-ranched *S. salar*, on the other hand, usually grow up in hatchery

TABLE I. Early experiences and types of later performances covered in this review

Early experience	Effect on later performance
Temperature during embryogenesis	Juvenile growth rate
Temperature during egg development	Sex determination
	Adult size
Egg size	Age at maturity
Paternal care	Egg size
Maternal condition and stress	Fecundity
Acidity in water	Survival and lifespan
Early density	Cognition and learning
Predator stress	Boldness and risk taking
	Partial migration

tanks where all competitors are of similar age and size, and there is little risk of serious injuries when fighting over resources. When fed, they rush to the feed and they appear to develop behavioural patterns during their first couple of months linking activity to aggressiveness and exploration tendency (Andriaenssens & Johnsson, 2013). In hatchery-produced salmonids, this behavioural syndrome appears to hold years after being released in nature (Fleming *et al.*, 1997; Réale *et al.*, 2010). Thus, liberated hatchery-produced salmonids are more often injured than wild conspecifics, which exhibit more cautious behaviours (Jonsson, *et al.*, 1990*a*; Biro & Stamps, 2008), as illustrated in experiments performed in spawning arenas with wild, farmed and sea-ranched *S. salar* (Fleming *et al.*, 1996; 1997).

Similarly, in three-spined sticklebacks *Gasterosteus aculeatus* L. 1758 social behaviours are partly experience based. Aggression from parents on newly hatched offspring can prepare their young ones for proper anti-predation behaviour. Males guard and tend the eggs, but only in habitats with predators, they chase away their offspring a few days after hatching. By this pursuit, they prime adequate anti-predator responses in the developing juveniles (Huntingford *et al.*, 1994). Thus, although genetic differences play an important role in expressions of personality traits (Sundström *et al.*, 2004), parental effects and gene–environment interactions further shape an individual's behaviour (Carere *et al.*, 2005; Stamps & Groothuis, 2010).

The mechanism inducing different social behaviours, such as those between wild and liberated hatchery fishes, is unknown. It was found, however, that cultured Pacific salmonids *Oncorhynchus* spp. have smaller brains than similar-sized wild conspecifics (Kihslinger & Nevitt, 2006; Kihslinger *et al.*, 2006). Furthermore, sensory organs, such as the lateral line system and eyes, can be modified during hatchery rearing and influence behavioural performances (Marchetti & Nevitt, 2003; Anras & Lagardere, 2004). Also, the brain–gene expression profiles in *S. salar* can be affected by the juvenile rearing environment with effects on which behavioural tactics adult fish use (Aubin-Horth *et al.*, 2005). Experiments have demonstrated that a year after hatching, juvenile *S. salar* reared in an impoverished tank environment had lower neural plasticity in the telencephalon and down-regulated neurogenic differentiation in one mRNA expression (transcription factor encoded by the *neuro1* gene) compared to similar juveniles with early experience from an enriched tank environment (Salvanes *et al.*, 2013). The exposure to the enriched environment produced fish with superior learning abilities as

exhibited by enhanced abilities to correctly locate a maze exit during 7 days of testing. Thus, there may be a link between neural plasticity gene expression markers and the spatial behaviour of fishes.

A difference in early social environment can also be the reason for differences in gene expression in the cooperatively breeding cichlid *Neolamprologus pulcher* (Trewavas & Poll 1952). Taborsky *et al.* (2013) compared the expression of four genes of the hypothalamic–pituitary–interrenal (HPI) axis in adults, which had been exposed to two early life social treatments 1·5 years prior to brain sampling. They found that early social experiences altered the programming of the stress axis, and suggested that the adult social behaviour was persistently modified by early life social experience. Behavioural effects of the early rearing environment for *S. salar* and brown trout *Salmo trutta* L. 1758 are currently tested in management-related experiments with the purpose of producing fishes with more natural behaviours (Näslund *et al.*, 2012; Hyvarinen & Rodewald, 2013).

There can also be trans-generational influence caused by environmental conditions encountered by parents resulting in heritable changes in the offspring as in the case of sheepshead minnow *Cyprinodon variegatus* Lacépède 1803. Here, elevated temperature experienced by either parent prior to fertilization modified offspring thermal reaction norms for growth (Salinas & Munch, 2012). It is not known how widespread this epigenetic effect is among fish species, but epigenetic effects are potentially important for offspring development. They may compensate for a poor start under some conditions, and such effects will probably be more keenly studied in the future. At the very least, epigenetic responses may be relevant in relation to climate change effects on organisms (Jonsson *et al.*, 2005; Finstad & Jonsson, 2012).

WHAT IT IS NOT

Early experience effects differ from 'seasonal compensation effects' that can occur when there is a reduction in population size in one season that results in a change in per capita rates in the following season. It also differs from compensatory effects where fishes, after periods of food shortage or unfavourable thermal conditions, can exhibit higher than normal growth rates restoring energy reserves (Arendt, 1997; Ali *et al.*, 2003; Gurney *et al.*, 2003). After periods of hunger, individuals can compensate for lost feeding opportunities in a subsequent hyperactive period. For instance, rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) starved for 3 weeks grew twice as fast as unstarved conspecifics when fed during the subsequent 3 weeks (Dobson & Holmes, 1984). Similarly, Johnsson & Bohlin (2005) showed compensatory growth in *S. trutta* during 1 month after a period of starvation. Fish kept on the restricted diet restored lost body mass and condition within a month. Compensatory growth is probably a mechanism by which fishes are able to pass energy thresholds associated with developmental switches, such as maturation or migration, and not a compensation for lost growth *per se* (Álvarez & Nicieza, 2005). Size can be vital in situations where the fish is predator or prey and hence influences the outcome of trophic interactions.

Developmental effects are not 'carry-over effects' which occur when processes in one season influence the success of an individual in the following season. For instance, fishes can increase their reproductive effort when well fed prior to spawning or skip spawning if food is scarce (Bunnell *et al.*, 2007; Kennedy *et al.*, 2008). In *S. trutta* and *S. salar*, male gonad size was found to decrease with migratory costs associated

with spawning (Jonsson & Jonsson, 2003, 2006). Bunnell *et al.* (2007) reported that in white crappie *Pomoxis annularis* Rafinesque 1818 females produced larger ovaries and eggs when better fed prior to maturation. Carry-over effects can be important for environmental adaptability, but are not reviewed here.

MECHANISMS

Phenotypically plastic reactions may be conveyed by enzymatic influence caused by abiotic or biotic characteristics of the environment. Changes can also be caused by learning, parental influence and through epigenetic effects influencing the physiology of the organism. Epigenetics refer to functionally relevant modifications of the genome that do not involve a change in the nucleotide (DNA) sequence (Holliday & Pugh, 1975; Riggs, 1975; Jones & Taylor, 1980), and may also be provided by the mother as a parental effect, be inherited or based on own experience (Singh *et al.*, 2012). These are all mechanisms with effects on phenotypically plastic reactions. The causes presented in this review are experiences encountered either *via* their parents or during egg incubation or early life, whereas the effects produced last through juvenile life or longer.

LEARNING AND MEMORY

Fishes learn from experience and can use the knowledge gained in decision-making. One well-known example of early learning is the salmonid memory of their natal area, which they use to find their way to the spawning grounds in a river they left years earlier for feeding in the ocean (Hasler & Scholz, 1983), but fishes do not only learn the location of their natal area, they also know how to navigate back to their home stream and natal area from distant feeding areas (Hansen *et al.*, 1993), whether this is with help of a cognitive map, magnetic orientation or olfactory cues (Quinn, 1980; Dittman & Quinn, 1996; Putman *et al.*, 2014). During navigation, they may use associations between different stimuli, such as the location of specific resources in relation to the position of landmarks (Warburton, 2003), and they can plan escape routes when threatened by a predator (Ebbeson & Braithwaite, 2012). Also, fishes can form mental maps in which they can encode both vertical and horizontal components (Holbrook & Burt de Perera, 2011), and they can integrate temporal and spatial information and use this to predict when and where specific events will occur (Reebs, 1996). By combining information, they can comprehend ways to respond or behave in complex situations encountered later in life.

There appear to be critical periods when the brain is most plastic and receptive to environmental influences (Knudson, 2004). The critical periods of development occur at key transitions from one life stage to the next, such as early postnatal development and puberty with heightened neural development (McCormick & Green, 2013; Stratman & Taborsky, 2014). Early life is important for the development of sensory processes and cognition where the fishes have to adapt to a range of foraging opportunities, to cope with varying predation threats and social interactions (Ebbeson & Braithwaite, 2012).

PARENTAL EFFECTS

Parental effects have traditionally been called maternal effects because effects transmitted *via* the mother were the first to be noticed and because paternal effects, other than

genetic effects transmitted *via* the father, were thought to be minimal or non-existent (Roach & Wulff, 1987; Rossiter, 1996). Recent studies, however, suggest that paternal effects may be more important than previously thought (*e.g.* insects: Giesel, 1986, 1988; Fox *et al.*, 1995; mammals: Clutton-Brock, 1991). Fathers can influence their young ones in ways such as through fertilization success and parental care, and thereby, they indirectly affect offspring competitive ability, growth and associated life-history traits.

A parental effect is any parental influence on offspring phenotype that cannot be attributed to offspring genotype, and to the action of non-parental components of the offspring's environment (Lacey, 1998). Parental effects occur when the phenotype of an individual is determined not only by its own genotype and environmental conditions experienced, but also by the parental phenotype and environment (Wright, 1969). A parental effect can be spawning at a more appropriate time or place, or a physiological effect such as the provisioning of a larger amount or higher quality yolk to the embryo, improving larval growth and survival (Stratman & Taborsky, 2014). It may also have longer-term effects such as influencing age at maturity or lifespan of the offspring (Heath & Blouw, 1998). It can be an epigenetic effect where the function, but not the base sequence of the genome, is changed. Studies have demonstrated that parental effects can have important ecological and evolutionary consequences (Reznick, 1991; Räsänen & Kruuk, 2007; Stratman & Taborsky, 2014).

In most organisms, progeny phenotypes tend to be influenced more by the genotype or environment of their mother than by the genotype and environment of their father (Heath *et al.*, 1999). Studies have demonstrated that parental effects can have important ecological and evolutionary consequences (Reznick, 1991; Räsänen & Kruuk, 2007). Variation in offspring size is one of the best understood mechanisms by which variation among females influences the phenotypes of progeny. In fishes, maternal (relative to paternal) effects are best documented.

In many fish species, juvenile and adult ecologies differ because the individuals grow through life, and thereby, their environmental requirements alter, thus changing their competitive abilities and predator susceptibility. Juveniles and adults of the same species may have more different ecological requirements than adults of different species (Werner, 1977). Therefore, fishes can undergo ontogenetic shifts in feeding niche, and juveniles can occupy a different niche from adults in a common habitat or juveniles and adults can be spatially separated (Werner & Gilliam, 1984; Jonsson & Jonsson, 1993). It is expected that organisms occupy the habitat that minimizes mortality rate over growth rate, rates which vary with time and size of the fish. For adults, precise forecasting of offspring conditions from the ambient environment can be difficult or even impossible if the two live in different habitats. Hence, females may programme their offspring to live in a similar environment they experienced when young, which quite reliably can predict their offspring's future environment. This situation can give rise to 'life stage-specific maternal effects', where the environmental conditions experienced by females during a certain life stage (*e.g.* the early juvenile stage) induce a maternal effect that affects the same life stage in the offspring generation (Kotrschal *et al.*, 2012).

An example of how maternal experience can influence offspring *via* non-genetic mechanisms is from a study of *G. aculeatus* (Giesing *et al.*, 2011). There, predator-exposed females produced larger eggs with higher cortisol content, and their juvenile offspring swam in tighter shoals (an anti-predator defence) than offspring of

non-exposed females. Thus, mothers exposed to an ecologically relevant stressor during egg formation can transfer a long-lasting effect to their progeny, which may be mediated by exposure to maternally derived cortisol. The results support the hypothesis that female *G. aculeatus* can influence development, growth and behaviour of their offspring *via* eggs to match their future environments.

EPIGENETIC EFFECTS

Phenotypic variation can result from an environmental effect on the genotype as an epigenetic change (Roberts & Gavery, 2012). Epigenetic effects can be involved in the differentiation of cell lines and trigger altered gene expression (Jablonka & Raz, 2009), and it can be induced by hybridization or environmental stress and contribute to adaptations to novel environments. Often, epigenetic effects are caused by conditions encountered by the embryo or larva, but can also be trans-generational effects caused by conditions experienced by the parents (*de facto* parental effect). Experiments with rats as a model organism have demonstrated permanent growth retardation in offspring nursed by mothers fed a low-protein diet (Desai & Hales, 1997). Also, the programming of liver metabolism can be changed as reflected by permanent changes in activities of key hepatic enzymes of glycolysis and gluconeogenesis, which bias the liver towards a 'starved' setting. Desai & Hales (1997) also reported an increase in the life span of offspring exposed to maternal protein restriction during the lactation period, and a decrease in life span when exposed to maternal protein restriction during gestation. The latter study revealed that hepatic metabolism and lifespan can be programmed by events during early life without involving changes in the nucleotide sequence.

The molecular basis of epigenetic effects involves modifications of the activation of certain genes, and proteins associated with DNA may be activated or silenced such as in genomic imprinting, where one of the two alleles of a gene is silenced and expressed in a parent-of-origin-specific manner (Jablonka, 2001). One of the mechanisms is DNA methylation, usually associated with inhibition of genetic transcription.

Changes in DNA methylation, unlike DNA mutations, can be influenced by the environment; they are stable at the time scale of an individual, and present different levels of heritability. These characteristics make DNA methylation a potentially important molecular process to respond to environmental change (Angers *et al.*, 2010). Other epigenetic effects on gene expression include histone- and RNA-based modifications such as microRNA, small interfering RNA, and spatial location of DNA and the organization of the chromatin matrix in the nuclear space, as well as three-dimensional templating mechanisms and self-sustaining loops (Matouk & Marsden, 2008; Richards *et al.*, 2010; Gräff *et al.*, 2011; Khrameeva *et al.*, 2012). Among these, DNA methylation is best studied.

DNA methylation affects many developmental processes responsible for phenotypic variation. The methylation occurs in certain regions of the genome, and refers typically to the addition of a methyl group to position 5 of cytosine bases when cytosine occurs adjacent to a guanine nucleotide (McGowan & Martin, 1997) but it is becoming increasingly evident that there may also be significant methylation in non-cytosine-guanin contexts, at least in pluripotent cell types and oocytes (Ramsahoye *et al.*, 2000; Tomizawa *et al.*, 2011). Addition of methyl groups is catalyzed by enzymes called DNA methyltransferases. DNA methylation stably alters the expression of genes in cells as cells differentiate from embryonic stem cells to specific tissues.

High levels of DNA methylation are associated with silencing of gene expression, and reduced methylation is linked to active gene transcription (Bird, 2002). Temperature can influence the intensity of the DNA methylation, and it occurs abundantly in polar marine species (Kakutani, 2002). The relative amount and location of DNA methylations vary across taxa. It is plausible that these marks can have different functions and different mechanisms of action across organisms and evolutionary time (Roberts & Gavery, 2012). Although implications of DNA methylation are well known, the fundamental understanding of its functioning in fishes is lacking (Simonet *et al.*, 2013).

Histone (proteins that package and order the DNA into structural units called nucleosomes) modifications also affect gene expression. Histone acetylation is a parallel to methylation, but whereas methylation is generally associated with inhibition, acetylation is associated with activation. Histone acetylation is important in regulating the structure and function of chromatin, and hence, the eukaryotic genome. Zhang *et al.* (2013) reported that histone deacetylation was involved in sex differentiation in rice-field eels *Monopterus albus* (Zuiew 1793). They suggested that histone modification in addition to DNA methylation may be widely used to drive natural sex change in teleosts and gonadal differentiation in vertebrates.

Most epigenetic changes occur within the course of one individual organism's lifetime, but they can be inherited trans-generationally (Chandler, 2007). They are the emergent properties of the genome and the response to its environment, both of which are heritable and mutable (Kutschera & Niklas, 2004).

EXAMPLES OF TRAITS AFFECTED BY EARLY EXPERIENCES

GROWTH AND SIZE

Most studies on effects of early influences on later growth have been performed with endotherms in relation to long-term consequences of early life stress and the resulting glucocorticoid exposure, maternal interactions, and foetal development (de Boo & Harding, 2006; Champagne, 2008). Strangely enough, fewer studies are on ectotherms, although their growth depends on environmental temperature (Schlichting & Pigliucci, 1998; Wootton, 1998) (Table II). In fishes, maximum individual growth rate increases with temperature to an optimum value, and then it decreases rapidly at higher temperatures (Elliott, 1994). The decrease at high temperature is probably because dissolved oxygen in the water decreases with increasing temperature whereas the fish's need for oxygen increases (Brett, 1952; Pörtner, 2010). This function allows ectotherms to maintain thermal homeostasis within a wide range of temperatures (Angilletta *et al.*, 2002). Also, thermal experience from the perinatal period can modulate the normal course of development and permanently alter phenotypes.

Temperature influences the rate of myogenesis (formation of muscular tissue), including composition of the functional structures within the cells, patterns of gene expression, number and size of muscle fibres, fibre diameters and myofibril areas (Johnston, 2006). From studies of *S. salar*, Stickland *et al.* (1988) reported that post-hatching embryos, incubated at higher temperatures, had larger, but fewer muscle fibres, than those incubated at lower temperatures. Large muscle fibres contain more myofibrillar material than smaller fibres. Campos *et al.* (2013) reported similar findings from studies of Senegalese sole *Solea senegalensis* Kaup 1858, and Steinbacher *et al.* (2011)

TABLE II. Early influence with delayed effects on juvenile growth. Experimental species and study cited are given

Influence	Experimental species	References
Embryonic temperature	*Rutilus meidingeri*	Steinbacher *et al.* (2011)
	Salmo salar	Finstad & Jonsson (2012)
	Danio rerio	Scott & Johnston (2012)
Early predator stress	*Oncorhynchus mykiss*	Bell *et al.* (2011)
Parental care	*Amphiprion melanopus*	Green & McCormick (2005)
Maternal maturation temperature	*Cyprinodon variegatus*	Salinas & Munch (2012)
Amount of yolk	*Simochromis pleurospilus*	Segers *et al.* (2012)

found that pearlfish *Rutilus meidingeri* (Heckel 1851) incubated at high temperature were larger at hatching than those incubated in colder water. The latter had reduced cell differentiation leading to smaller hatchlings, which secured a larger pool of muscle pre-cursor cells used for enhanced post-hatchling growth, finally resulting in larger adults.

Somatic growth is determined by the surplus energy of the organism, *i.e.* energy not used for activity, maintenance and specific dynamic action. The cost of mainte-nance is influenced by the standard metabolic rate (Burton *et al.*, 2011), and Álvarez *et al.* (2006) reported that the standard metabolic rate of juvenile *S. trutta* changed in response to temperature during larval development, which parallels the observation that subsequent juvenile growth varies depending on temperature during embryogene-sis. This relationship holds for *S. salar* and some other species (Finstad & Jonsson, 2012). Juvenile *S. salar* developed from eggs incubated during winter in unheated water (2–4° C) grew less well in water warmer than 17° C than conspecifics with embryogenesis in water heated to 6–8° C. This finding explains the observation that cohorts of *S. salar* incubated during relatively warm winters grew better as juveniles in fresh water and migrated at a younger age to the sea, than those with embryonic development during colder winters. This difference in juvenile growth was independ-ent of the water temperature in the subsequent summer (Jonsson *et al.*, 2005). This early effect on juvenile growth might have been considered in a recent experiment with Atlantic cod *Gadus morhua* L. 1758. Fish reared from young ones caught in the warmer Clyde Sea on the west coast of Scotland grew faster than those from the colder St Andrews Bay, when the young ones were brought together under similar controlled conditions (Harrald *et al.*, 2010). The authors viewed this as an example of genetic differentiation between populations, but an environmentally induced epige-netic effect would have given a similar result. Thermal effects during egg incubation can last much longer than through the larval period and should be taken into considera-tion when comparing population-specific adaptations of fishes. This view is supported by the observation from another gadid, haddock *Melanogrammus aeglefinus* (L. 1758); Martell *et al.* (2005) reported that temperature during embryogenesis influenced sub-sequent growth. Similarly, Korwin-Kossakowski (2008) reported that growth of young common carp *Cyprinus carpio* L. 1758 was enhanced by incubating the eggs in rela-tively warm water, indicating that this may be a common phenomenon in teleosts.

Egg incubation temperature also influences later thermal acclimation. Scott & John-ston (2012) used *D. rerio* as a model species. They observed that temperature during embryogenesis influenced the thermal reaction norm for growth, and that differences

in expression were observed for individual genes involved in energy metabolism, blood vessel formation (angiogenesis), cell stress and muscle contraction. Also, predatory stress can influence later growth. Juvenile *G. aculeatus* exposed to cues of an *O. mykiss* predator grew faster, but were smaller at adulthood than corresponding juveniles prevented from exposure to *O. mykiss* (Bell *et al.*, 2011). The smaller size probably resulted from a deferred cost of early rapid growth with subsequent reduced age and size at maturity (Alm, 1959; Jonsson *et al.*, 2013).

Maternal and paternal effects can influence size and growth of fishes. In tropical clownfish *Amphiprion melanopus* Bleeker 1852, Green & McCormick (2005) observed that larval size at metamorphosis was primarily affected by maternal and paternal effects. Paternity explained 52% of the variance in growth rates, while the combination of paternity, maternity and temperature explained 30%. This strong paternal influence may be due to the extensive role males play in nest-tending coupled with the relatively long embryonic duration of the species.

Trans-generational thermal effects experienced by the parent prior to egg fertilization can also translate into significant changes in the shape of offspring reaction norms for growth (Mousseau & Fox, 1998). Salinas & Munch (2012) reported that female *C. variegatus* kept at either 24, 29 or 34° C for 30 days during egg maturation produced offspring that grew best at the temperature experienced by their mothers. The change in growth over a single generation (*c.* 30%) exceeded the single-generation rate of adaptive evolution by an order of magnitude. In this species, mothers adaptively programmed their offspring for maximal growth at the present temperature.

Growth hormone expressions can also influence juvenile growth. Segers *et al.* (2012), using the mouth breeding cichlid *Simochromis pleurospilus* Nelissen 1978 as a model species, reported that young ones originating from small eggs had higher growth hormone receptor expression levels causing juveniles from small eggs to grow faster than those from larger eggs. A similar relationship may explain Berejikian *et al.'s* (2001) finding that offspring growth rate and egg size in Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) were negatively correlated.

Presence of specific metabolic enzymes, such as different trypsin isozymes, can influence growth. Trypsin is a key digestive protease, which is sensitive to environmental change and influences feed utilization and growth during the life cycle (Rungruangsak-Torrissen & Male, 2000). The trypsin isozyme variants influence maintenance ration and the capacity for protein synthesis in white muscle with effects on growth, size and other life-history variables. The genetic mechanism for flexible trypsin production is unknown, but Jump & Clark (1999) maintained that environmental factors may interact with the genome and allow cells to adjust to an on and off switch gene expression, possibly influenced by DNA methylation. Sainz *et al.* (2005), on the other hand, concluded from a study of isotrypsin patterns that the regulation was quantitative not qualitative, and that changes in trypsin activity and in trypsin mRNA by internal and external stimuli must be related to changes in the rate of synthesis of the established isoenzymes. In any case, trypsin regulation is one possible mechanism by which growth is influenced by temperatures experienced by the embryos.

From endotherms, it has been observed that maternal hormonal responses can alter the offspring phenotype (Kaiser & Sachser, 2009). For instance, maternal androgens deposited in avian eggs provide a flexible mechanism of non-genetic inheritance by which the mother can adjust the development of some over the others

(Groothius *et al.*, 2005). In fishes, the physiological condition of mothers during gametogenesis can influence offspring quality of damselfish *Pomacentrus amboinensis* Bleeker 1868 (McCormick, 1998). The reason may be that competitors and predators can elevate maternal cortisol levels and consequently influence larval morphology through a stress-related response. Thus, behavioural interaction regimes can determine larval quality and potentially govern a female's contribution to the next generation.

SEX RATIO

Environmentally influenced sex determination has stimulated much research. In most fish species, sex is genetically determined, but in some, environmentally influenced sex differentiation has been documented. Water temperature is the main environmental determinant of sex, and also water acidity (Heiligenberg, 1965; Rubin, 1985; Francis & Barlow, 1993), fish density and social interactions, growth rate and contaminants can affect sex ratios (Baroiller & D'Cotta, 2001; Baroiller *et al.*, 2009*a*; Sandra & Norma, 2010; Siegfried, 2010) (Table III). Thermal influences are best studied.

Thermal influence

Thermal sex determination occurs in several species. In some cases, the sex is changed if eggs or larvae are exposed to extremely high temperatures, but not under normal conditions, such as in sockeye salmon *Oncorhynchus nerka* (Walbaum 1972), *O. mykiss*, *O. latipes*, Nile tilapia *Oreochromis niloticus* (L. 1758) (Tessema *et al.*, 2006) and *D. rerio*. In other cases, sex is influenced by temperatures individuals typically encounter in nature. This is better known from reptiles where temperature influences sex determination by modulating the activity of steroidogenic enzymes affecting the hormonal environment of the embryo inducing masculinization or feminization (Janzen, 1994), but it also occurs among teleosts. Ospina-Álvarez & Piferrer (2008) reported temperature-influenced sex differentiation in 33 cichlids and a few other species (Table III). In flatfishes of the genus *Paralichthys*, larvae of genetic females may exhibit sex reversal when exposed to warm water (Montalvo *et al.*, 2012*a*, *b*). Also, *O. niloticus* may exhibit sex reversal in natural lakes. The temperature sensitivity is under genetic control, and surplus males in temperature-treated groups can be selected as a quantitative trait (Rougeot *et al.*, 2008; Baroiller *et al.*, 2009*b*; Lozano *et al.*, 2013). Recently, Wedekin *et al.* (2013) reported that the frequency of male European grayling *Thymallus thymallus* (L. 1758) increased with increasing temperature in Lake Thun, Switzerland, and the authors speculate about thermally influenced sex determination in this species.

In cases of thermally influenced sex differentiation, the sex is determined during a sensitive period of early development (Valenzuela *et al.*, 2003). Typically, species without consistent genetic differentiation produce relatively more males as the temperature increases (Ospina-Álvarez & Piferrer, 2008; Hasyashi *et al.*, 2010), but in the channel catfish *Ictalurus punctatus* (Rafinesque 1818) (Patino *et al.*, 1996), Korean rockfish *Sebastes schlegeli* Hilgendorf 1880 (Omoto *et al.*, 2010), European seabass *Dicentrarchus labrax* (L. 1758) (Baroiller & D'Cotta, 2001) and possibly in dwarf perch *Micrometus minimus* (Gibbons 1854) high temperatures induce relatively more females. In the last species, Schultz (2008) observed that broods developing at low temperatures early in the season produced relatively more males than those developed in warmer water later in the season. In the olive flounder *Paralichthys olivaceus*

TABLE III. Environmental variables affecting sex determination in fishes

Variables	Species	References
Water acidity	*Pelvicachromis pulcher*	Rubin (1985)
	Pelvicachromis taeniatus	
	Pelvicachromis subcellatus	
	Apistogrammus borelli	
	Apistogrammus cacatuoides	
	Apistogrammus diplotaenia	Römer & Beisenherz (1996)
Temperature	*Apistogrammus* spp.	Römer & Beisenherz (1996); Ospina-Álvarez & Piferrer (2008)
	Menidia menidia	Ospina-Álvarez & Piferrer (2008)
	Menidia penninsulae	
	Odontesthes bonariensis	
	Odontesthes argentinensis	
	Haplosterum littorale	
	Poeciliopsis lucida	
	Limia melanogaster	
	Oncorhynchus nerka	Craig *et al.* (1996); Azuma *et al.* (2004)
	Oncorhynchus mykiss	Magerhans *et al.* (2009)
	Oryzias latipes	Selim *et al.* (2009)
	Oreochromis niloticus	Tessema *et al.* (2006)
	Danio rerio	Abozaid *et al.* (2012); Villamizar *et al.* (2012)
	Ictalurus punctatus	Patino *et al.* (1996)
	Sebastes schlegeli	Omoto *et al.* (2010)
	Dicentrarchus labrax	Baroiller & D'Cotta (2001)
Growth	*Danio rerio*	Lawrence *et al.* (2008)
	Rutilus rutilus	Paull *et al.* (2009)
Density	*Macropodus opercularis*	Baroiller & D'Cotta (2001)
Growth, density or social influence	*Anguilla* spp.	Krueger & Oliveira (1999); Davey & Jellyman (2005)
	Paralychthys lethostegma	Luckenbach *et al.* (2003)
	Ichthyomyzon gagei	Beamish (1993)

(Temminck & Schlegel 1846), both high and low temperatures induce monosex male populations while intermediate temperatures yield a 1:1 sex ratio (Baroiller & D'Cotta, 2001).

The effect of temperature on sex determination can depend on whether temperature is stable or varies between day and night. Villamizar *et al.* (2012) found that temperature varying between 24 and 28° C during day and night gave more females in *D. rerio* than at either temperature when stable.

Physiological regulation

In gonochoristic fishes, steroid hormones, oestrogens in females and 11-oxygenated androgens in males regulate key physiological steps of gonadal sex differentiation

(Baroiller & D'Cotta, 2001). The temperature-sensitive cytochrome P450-aromatase enzyme catalyzes the oestrogen biosynthesis and feminization by conversion of androgens to oestrogens as, for example, demonstrated for southern flounder *Paralichthys lethostigma* Jordan Gilbert 1884 (Montalvo *et al.*, 2012*a*, *b*). Furthermore, in *O. niloticus* and *P. olivaceus*, the aromatase gene expression is down-regulated by masculinizing temperature treatments. Masculinization at high water temperature has been ascribed to stress and elevated cortisol concentration during gonadal sex differentiation, as in larval *P. olivaceus* (Yamaguchi *et al.*, 2010). Cortisol may promote the level of 11-ketotesterone, the main androgen in fishes, and thereby induce the masculinization as demonstrated for Argentinian silverside *Odontesthes bonariensis* (Valenciennes 1835) (Fernandino *et al.*, 2012). In Atlantic silverside *Menidia menidia* (L. 1766), Blazquez & Somoza (2010) suggested that an aromatase enzyme encoded by the *cyo19a1b* gene may be involved in this process. A form of this enzyme occurs in high concentrations in the brain of teleosts, and may be involved in the conversion of androgens into oestrogens and thereby in feminizing fishes at low temperature. In experiments with *D. labrax*, it was observed that at high temperatures juvenile males have double the DNA methylation levels of females in the promotor region of the gonadal aromatase (Navarro-Martin *et al.*, 2011). Exposure to high temperatures increased the promotor methylation levels of females inhibiting development of ovaries, and DNA methylation at high temperature may be an essential component of the mechanism of temperature-dependent sex determination of the species. As mentioned earlier, histone deacetylation appears to be involved in sex differentiation of *M. albus* (Zhang *et al.*, 2013).

Ecological significance

The adaptive significance of environmentally induced sex differentiation is not well understood. One possibility is that it is a remnant trait still present and retained because the cost is small relative to the more common genetic sex determination. It is assumed, however, that environmental sex reversal overpowering genetic sex determination probably has fitness costs. Senior *et al.* (2012) meta-analytically combined the results of 78 studies of chemically induced sex reversal, and found that the fitness of the fish was reduced at the time of exposure. Exposed individuals exhibited a smaller size and a smaller gonado-somatic index than unexposed individuals. This result held independent of growth rate of the fish.

Charnov & Bull (1977) predicted that selection would favour environmentally induced sex determination over chromosome-based sex determination when the fitness of the sex varies among environments. This model appears to hold for *M. medinia* (Conover, 1984). There, offspring produced early in the breeding season maximize relative fitness if they become female, and offspring produced late in the breeding season maximize relative fitness by becoming male, and populations at different latitudes compensate for differences in thermal environment and seasonality by adjusting the response of sex ratio to temperature (Conover & Heins, 1987). Furthermore, Conover *et al.* (1992) reported evidence suggesting that environmental sex determination can evolve in response to selection. Also for reptiles, there is some evidence that this mechanism can be adaptive (Warner & Shine, 2008), but for most species, it is an open question if and to what degree environmentally influenced sex differentiation is adaptive or not.

TABLE IV. Early influences with delayed effect on life-history variables. Experimental species and study cited are given

Influence	Characteristic influenced	Species	References
Parental density	Egg size	*Heterandria formosa*	Leips *et al.* (2009)
Early growth	Egg size	*Salmo salar*	Jonsson *et al.* (1996)
		Salvelinus leucomaenis	Morita *et al.* (1999)
		Oncorhynchus masou	Tamate & Maekawa (2000)
		Coregonus albula	Gregersen *et al.* (2011)
Early growth	Lifespan	*Gasterosteus aculeatus*	Inness & Metcalfe (2008); Lee *et al.* (2013*b*)
Early growth	Partial migration	*Salmo trutta*	Olsson *et al.* (2006)
Early spawning	Partial migration	*Morone americanus*	Kerr & Secor (2010)
Maternal feeding	Egg size	*Simochromis pleurospilus*	Taborsky (2006)
Maternal predator experience	Egg size	*Eretmodus cyanostictus*	Segers & Taborsky (2012)
		Gasterosteus aculeatus	Giesing *et al.* (2011)

LIFE-HISTORY TRAITS

This section summarizes effects of early experiences on life-history traits (Table IV). One of the most well-known examples is that of increased early growth rate that leads to earlier age-at-life-stage transitions such as age when a fish exhibits dietary change or shifts to a better feeding habitat and seaward migration in anadromous species (Jonsson & Jonsson, 1993; Jonsson *et al.*, 1999). Another such transition is during maturation of the fish.

Age at maturity

Early maturation is related to juvenile growth, size and fat storage, where both fast initial growth and high lipid density reduce age at maturity. This was demonstrated for a number of freshwater species by Alm (1959) and Day & Rowe (2002) and particularly well documented for salmonid species, *e.g.* Arctic charr *Salvelinus alpinus* (L. 1758) (Jonsson & Hindar, 1982; Forseth *et al.*, 1995), *S. trutta* (Alm, 1959; Jonsson, 1985), *S. salar* (Thorpe, 1986; Berglund, 1992), masu salmon *Oncorhynchus masou* (Brevoort 1856) (Silverstein *et al.*, 1997), *O. tshawytscha* and coho salmon *Oncorhynchus kisutch* (Walbaum 1792) (Vøllestad *et al.*, 2004). In salmonids, winter growth and fat content in the diet as well as genetic constitution also influence age at maturity (Gjerde, 1984; Jonsson *et al.*, 2012, 2013). Thus, factors influencing early growth rate can be reflected in age at maturity.

Egg size and fecundity

It has been reported that females growing fast at early age produce more, but smaller eggs, than more slow growing conspecifics in *S. salar* (Jonsson *et al.*, 1996), *S. trutta* (Lobon-Cervia *et al.*, 1997), *O. masou* (Tamate & Maekawa, 2000), white-spotted charr *Salvelinus leucomaenis* (Pallas 1814) (Morita *et al.*, 1999) and European vendace

Coregonus albula (L. 1758) (Gregersen *et al.*, 2011), but no such effect was found in *O. tshawytscha*, *O. kisutch* and *O. mykiss* (Quinn *et al.*, 2004, 2011). This discrepancy may indicate that it is not growth *per se*, but a factor stimulating growth, which caused the observed variation in egg size. As discussed earlier in this review, temperature during embryogenesis enhances juvenile growth and is regularly used in hatcheries to advance developmental rates (Finstad & Jonsson, 2012).

Relationships between egg size, fecundity and growth history are also revealed by studies of latitudinal clines. In *S. trutta*, *O. kisutch* and *O. masou*, egg size is typically larger and egg number lower at more northerly latitudes where early growth is lower (Fleming & Gross, 1990; Jonsson & Jonsson, 1999; Morita *et al.*, 2009). This correlation, however, may not be consequential, but rather, influenced by factors influencing growth rate, such as early temperature. Bownds *et al.* (2010) tested whether optimal offspring size differs between thermal environments, and if this provided a direct way of assessing the adaptive significance of temperature-driven variation in egg size in *D. rerio*. The effects of offspring size on performance were highly variable among life-history stages and dependent on the thermal environment; offspring size positively affected performance at some temperatures, but negatively at others. These data were used to generate a simple optimality model; the model predicted that mothers should produce the largest offspring at the lowest temperature, offspring of intermediate size at the highest temperature and the smallest offspring at the intermediate temperature. An experiment showed that the rank order of observed offspring sizes produced by mothers matched the predictions. The mothers adaptively manipulate the size of their offspring in response to thermally driven changes in offspring performance and highlight the utility of optimality approaches for understanding offspring size variation. Also, Iguchi (2012) examined egg size variation. Two populations of ayu *Plecoglossus altivelis* (Temminck & Schlegel 1846) were studied from the Lake Biwa system, Japan, where two streams with different temperatures showed similar maternal body sizes and hatchling sizes, but the eggs were larger in the colder stream. An experiment that used eggs from a single clutch showed that smaller hatchlings were obtained with a lower incubation temperature, indicating that the effect of differences on hatchling size can be cancelled out by variations in incubation temperature.

Lee *et al.* (2013*a*) tested if accelerated or decelerated early growth, caused by a short-term change in temperature, had fitness costs for *G. aculeatus*. Although the fish at adulthood were equal in size, those compensating for low growth by a subsequent accelerated growth rate had reduced reproductive investment (males: reduced sexual ornaments and speed of building nests; females: reduced clutch size, egg size and egg production per year). Thus, *G. aculeatus* with a decelerated growth trajectory showed improved breeding allocation.

Lobon-Cervia *et al.* (1997) reported that the number of eggs of first-time spawners was fixed during their first year of life, whereas the egg size was influenced by second-year growth. Also, according to Morita *et al.* (1999) and Tamate & Maekawa (2000), fast growth during the second year was associated with large eggs in the adult fishes, but the latter authors did not observe any associated effect on egg number. The influence of early growth history on reproductive traits is not only confined to salmonids, but also reported from other species. In a study of *S. pleurospilus*, Taborsky (2006) found that females raised in a poor environment produced larger young ones than females raised without food limitations. This maternal boost was due to a higher investment in eggs and to faster larval growth. As in *S. salar*, mothers appear to prepare

their offspring for rearing conditions similar to those they encountered as juveniles. This may be an adaptation in some species where the juvenile and adult environments are very dissimilar (Jonsson *et al.*, 1996; Taborsky, 2006; Burton *et al.*, 2013). It may also be advantageous for individuals colonizing new habitats with a different thermal regime so that they can modify their reproductive allocation to the novel conditions. Moreover, in a gradually changing climate, this phenotypically plastic mechanism can produce a more rapid change in reproductive investment than can be obtained through natural selection.

The behavioural mechanisms responsible for context-dependent fitness differences were studied in *S. pleurospilus* (Segers & Taborsky, 2011). Larger eggs gave rise to larger young ones with higher burst swimming speed. Food ration greatly influenced long-term growth, while egg size predominantly affected early fish size. Egg size and food ration interactively affected hiding and foraging behaviours of the fish. In the low-food treatment, individuals from small eggs spent less time in shelter and exhibited a higher commitment to foraging than individuals from large eggs. In a natural setting, this should increase predation risk of young ones originating from small eggs, particularly in hostile and nutrient-poor environments. When food was abundant, juveniles behaved similarly, irrespective of egg size. Thus, egg size affected juvenile growth and behaviour differently in different environments. While it is well established that large egg size raises offspring fitness in harsh environments, this study suggests that this advantage arose through risk-averse behaviour linked to offspring size.

Egg size is known to affect growth rate of young *S. alpinus*, and possibly also behaviour, but these effects appear to decrease with time and are minimized by the effects of social factors (Leblanc *et al.*, 2011). Fish hatching from large eggs were more mobile and foraged more than fish developed from smaller eggs. Social environment also affected foraging behaviour, mobility and space use. Group-living *S. alpinus* were more mobile, foraged more and responded faster to food delivery than isolated fish.

On the other hand, fishes do not always produce large eggs in hostile environments (Morrongiello *et al.*, 2012). Southern pygmy perch *Nannoperca australis* Günther 1861 inhabit a diversity of streams along gradients of environmental quality, variability and predictability. Populations inhabiting increasingly harsh streams produced more numerous and smaller eggs. The within-female egg size variability increased as environments became more unpredictable. The authors argued that egg size had only a minor influence on offspring fitness in harsh environments. Instead, maternal fitness was maximized by producing many eggs. The increased variability in size may be an example of bet hedging. Koops *et al.* (2003) found support for the hypothesis that egg size variability increased as the environmental predictability decreased. Einum & Fleming (2004), however, maintained that within-clutch variation, at least in salmon, is more likely a reflection of the direct influences of the rearing environment on a female's ability to allocate resources evenly, and is not an evolutionary adaptation.

Predator stress may also influence the size of the eggs produced. Segers & Taborsky (2012) reported that predator cues perceived by the mouth breeding striped goby cichlid *Eretmodus cyanostictus* (Boulenger 1898) produced heavier eggs, but smaller clutches, than conspecific females without prior predator experience. Thus, also in this species, mothers appear to have the ability to prepare offspring for challenges they may meet after birth by adjusting the amount of yolk in their egg, and thereby maximizing their fitness. Similarly, in *N. pulcher*, the mothers adjust the size of propagules to the selective forces to which the offspring can be exposed. When offspring are cared for by

parents or alloparents, protection may reduce the predation risk for the young ones, which may allow mothers to invest less per single offspring. In *N. pulcher*, brood care helpers protect group offspring and reduce the latters' mortality rate. With more helpers present, females can reduce their investment per egg (Taborsky *et al.*, 2007).

Is there any paternal effect on offspring success? Apparently, it is present in *D. rerio* (Uusi-Heikkila *et al.*, 2012). In the laboratory, females and males from four size groups were allowed to spawn freely. As expected, larger females produced more eggs and larvae with larger yolk sac than smaller females, but male body size further contributed to *D. rerio* reproductive success: offspring sired by large males exhibited higher hatching probability and these offspring hatched earlier and larger than offspring fertilized by small males. The largest males, however, experienced lower mating success and received fewer eggs than males of the smaller size classes. Although little studied, male size may be more important for offspring success than previously expected.

Partial migration

Partial migration is the divergence of a population into migratory and resident contingents of the same species (Jonsson & Jonsson, 1993). It has been demonstrated that early growth influences whether a fish from such populations becomes migratory or not. For instance, Olsson *et al.* (2006) showed experimentally with reciprocally transplanted *S. trutta* between two sections in a river that migratory behaviour developed depending on early density and early individual growth rate. In river sections with high *S. trutta* densities and low specific growth rates, the fish tended to become migratory. Conspecifics from low density sections where the initial growth rate was high tended to stay resident. This result was confirmed in rearing experiments with variable feeding regimes showing that the migration of *S. trutta* was environmentally induced (Wysujack *et al.*, 2009). Furthermore, from studies on white perch *Morone americana* (Gmelin 1789), Kerr & Secor (2010) reported that the migratory fish tended to originate from early spawned larval cohorts characterized by slow growth compared with later spawned cohorts with fast initial growth as revealed by otolith microstructure. Possibly, there are latent effects on partial migration of *M. americana* related to spawning phenology, its interaction with temperature and resultant larval growth rates. The migratory propensity may be controlled by a threshold switch-point that determines whether a migratory or a resident phenotype is expressed, and growth rate during early life may be one characteristic influencing the choice made. Decisions about migration, however, may be also taken at later occasions depending on the energetic state of the individuals (Forseth *et al.*, 1999).

Survival and lifespan

There is a positive correlation between early growth rate and lifespan (Metcalfe & Monaghan, 2003; Inness & Metcalfe, 2008). Faster growth in early life is associated with reduced length of life span. For instance, Lee *et al.* (2013*b*) exposed *G. aculeatus* briefly in cold or warm water to deflect young fish from their normal growth trajectories and showed that increased early growth reduced the life span while growing more slowly prolonged lifespan.

Maternal condition may also influence offspring survival. In the coral reef fish *Acanthochromis polyacanthus* (Bleeker 1855), good condition parents produced progeny with increased survival compared to parents in poorer condition

(Donelson *et al.*, 2008). The offspring from parents in good condition were larger at hatching, had larger yolk reserves and exhibited increased survival. Larger size is expected to provide benefits to offspring through reduced susceptibility to size-selective mortality. The range of offspring characteristics modified by parental condition can thus result in a greater proportion of offspring from good condition parents recruiting to the population.

BEHAVIOUR

This section summarizes behavioural effects of early influences (Table V). Some of these effects, such as those of social and predator avoidance behaviour, have growth and life-history consequences which were dealt with in preceding sections.

Social behaviour towards conspecifics

Phenotypic traits of parents can affect patterns of development in their offspring (Mousseau & Fox, 1998; McAdam *et al.*, 2002). This may be because the progeny develop in an environment chosen by their parents or social learning from the behaviour of their parents (Rossiter, 1996). Rearing in an enriched environment facilitates learning about novel prey items in *S. salar* (Brown *et al.*, 2003) and *G. morhua* (Braithwaite & Salvanes, 2005; Salvanes & Braithwaite, 2005), and competitive ability and behavioural variation in *O. mykiss* (Berejikian *et al.*, 2001; Lee & Berejikian, 2008). Experience of a varying and changeable environment appears to teach the fish flexible behaviours. Also, social learning with effects on the behaviour of the adults can be influenced by density at early rearing. Experiments with guppies *Poecilia reticulata* Peters, 1859 showed that individuals kept at low density during early life had greater shoaling tendency and more effective use of socially learned information. They were quicker to locate food in a maze task and had better learning skill than conspecifics reared at higher density (Chapman *et al.*, 2008). *Poecilia reticulata* reared at higher densities were less effective because of poorer capacity for watching and learning from shoal mates. Hatchery *S. trutta* are typically reared at high densities, but in an experiment where the fish were reared at lower, more natural densities, they were twice as likely to survive after release into a natural stream (Brockmark & Johnsson, 2010). Developing in a less crowded juvenile environment had a positive effect on the cognitive ability and overall survival to adulthood.

Anti-predator behaviour and risk taking

Predator avoidance behaviour can be influenced by early experience (Goodey & Liley, 1986). Experiments have shown that *P. reticulata* chased when young by adult conspecifics required significantly more attacks before they were captured than either *P. reticulata* without early experience of being chased or *P. reticulata* exposed to only visual or chemical cues associated with chasing by adults. Thus, conditioning of predator-avoidance behaviour by early exposure to chasing by potential predators, may be an advantage in physically and biotically heterogeneous environments occupied by *P. reticulata*, and chasing by adult conspecifics may provide part of the learning experience (cf. survival and lifespan).

Prey species may learn the identity of the predator early in life and use this when later approached by the predator (Lönnstedt *et al.*, 2012). Both visual and olfactory

TABLE V. Early influences with delayed effect on later behaviour. Experimental species and study cited are given

Influence	Characteristic influenced	Species	References
Variable feeding	Learning ability	*Simochromis pleurospilus*	Kotrschal & Taborsky (2010)
Rich rearing environment	Learning ability	*Salmo salar*	Brown *et al.* (2003)
		Gadus morhua	Braithwaite & Salvanes (2005); Salvanes & Braithwaite (2005); Strand *et al.* (2010)
Rich rearing environment	Competitive ability	*Oncorhynchus mykiss*	Berejikian *et al.* (2001)
	Behavioural variation	*Oncorhynchus mykiss*	Lee & Berejikian (2008)
Early habitat complexity	Navigation skill	*Salmo salar*	Salvanes *et al.* (2013)
Unpredicatble early environment	Boldness and exploratory behaviour	*Poecilia reticulata*	Chapman *et al.* (2010)
Early density	Shoaling tendency	*Poecilia reticulata*	Chapman *et al.* (2008)
Early chased and predator experience	Increased predator avoidance	*Poecilia reticulata*	Goodey & Liley (1986)
		Pomacentrus wardi	Lönnstedt *et al.* (2012)
Maternal predator experience	Decreased predator avoidance	*Gasterosteus aculeatus*	McGhee *et al.* (2012)
Maternal stress	Decreased feeding efficiency	*Salmo salar*	Eriksen *et al.* (2011)
Maternal stress	Schooling	*Gasterosteus aculeatus*	Giesing *et al.* (2011)
Adult presence	Increased aggressiveness and submissiveness	*Neolamprologus pulcher*	Arnold & Taborsky (2010)
Foster mother of another species	Mate preference	*Haplochromis pundamilia* *Haplochromis nyererei*	Verzijden & Cate (2007)

cues help the prey recognize the predator. Two to three week old coral reef damselfish *Pomacentrus wardi* Whitley 1927 were exposed to a high or low food ration and conditioned to recognize the olfactory cues (odours) and visual cues from two common benthic predators, the moon wrasse *Thalassoma lunare* (L. 1758) and sand lizard-fish *Synodus dermatogenys* Fowler 1912. Feeding history strongly influenced their

willingness to take risks in the natural environment. Conditioning in the laboratory with visual, olfactory or both cues from predators led fishes in the field to display risk-averse behaviours compared with fishes conditioned with sea water alone.

On the other hand, *G. aculeatus* maternal exposure to predation risk decreases offspring anti-predator behaviour and survival (McGhee *et al.*, 2012). Gravid females were exposed to a model predator or not, and the offspring's behaviour and survival were compared when they were alone with a live predator, the same type of predator that threatened their mothers. Offspring of predator-exposed mothers were less likely to orient to the predator and were more easily caught than offspring from unexposed mothers. The strength and direction of the maternal effect on offspring survival, however, depended on offspring size. Specifically, the larger the offspring from predator-exposed mothers, the more vulnerable they were to predation compared to offspring from unexposed mothers. These stress-mediated maternal effects can have non-adaptive consequences for offspring when they find themselves alone with a predator.

Inherited inter-individual variation in metabolic rate exists in a wide range of species, and there is a relationship between metabolic rate and risk taking in *D. labrax* (Killen *et al.*, 2012), but boldness and risk taking also have strong environmental components that affect the economy and adequacy of individual reactions to social challenges (Brown *et al.*, 2007). Environment may influence aggressive and submissive behaviours, linked to boldness through an early behavioural syndrome (Andriaenssens & Johnsson, 2013). In experiments with *N. pulcher*, Arnold & Taborsky (2010) showed that juveniles raised with adults exhibited more aggressive and submissive behaviours to each other than those raised with siblings only. The strength of the treatment effects depended on the opponent's social experience, and contests were terminated earlier only when both opponents had been raised with adults.

Unpredictability in early food supply can induce boldness in fishes as demonstrated by Chapman *et al.* (2010) in experiments with *P. reticulata*. Fishes with early experience of unpredictable environments were bolder and more exploratory than those reared in predictable environments. Individuals with early experience of unpredictability spent significantly less time associating in shoals with conspecifics. Also, early density can influence the tendency to shoal.

Effects of early rearing on breeding performance were studied by Fleming *et al.* (1997). They used *S. salar* in semi-natural spawning arenas by use of a split experimental design and showed that fish deprived of an early social environment with stronger competitors and predators did not retreat from competition when they met stronger contesters. In their experiments, they matched wild and sea-ranched *S. salar* of similar genetic background. The sea-ranched fish were tank reared in a hatchery without contact with larger fish. They were liberated at age 1 year when they migrated to sea for feeding in the North Atlantic Ocean together with natural river-produced juveniles. Thus, the sea-ranched fish were deprived of early, juvenile river experience. They did not compete for food among fish of different sizes and strengths. Both the natural and sea-ranched *S. salar* returned from the ocean 1 year later for spawning in the River Imsa. Although levels of aggressive behaviour were similar, the sea-ranched hatchery males were involved in more prolonged aggressive encounters and incurred greater wounding and mortality than wild males. Furthermore, the hatchery-produced males were less able to monopolize spawnings, and as a result, they only achieved 51% of the reproductive success of similar sized wild males. This reproductive inferiority varied directly with the male density and bias in the sex ratio, reflecting the intensity of male

breeding competition. A lower intensity of female than male competition was probably responsible for the lack of differences in breeding performance between hatchery produced and wild females.

In *S. salar*, maternal stress can affect the boldness and social dominance of the progeny. Eriksen *et al.* (2011) simulated maternal stress by giving the females intraperitoneal cortisol implants 1 week prior to fertilization of the eggs. Behavioural tests on the offspring 1·5 years after hatching demonstrated that those from the cortisol-implanted females made more unsuccessful feeding attempts than offspring from control females. There was no difference in social dominance between controls and the progeny of cortisol-treated fish. There were, however, higher proportions of individuals with bite marks in the cortisol group. Offspring of the cortisol-treated females that gained high dominant ranks were more aggressive than control winners. During acute confinement stress, offspring from cortisol-implanted females also showed a reduction in the proportion of time they were moving compared with the controls. Thus, the maternal endocrine state at spawning can affect several aspects of progeny behaviour.

Cognition

Increased habitat complexity can promote the cognitive ability of fishes. *Gadus morhua* reared in tanks with cobble stones and artificial kelp on the bottom was more adept at learning how to forage on novel prey than those reared in bare tanks (Strand *et al.*, 2010). Also, habitat enrichment improved navigation skills in *S. salar* (Salvanes *et al.*, 2013). Habitat-enriched fish were faster at finding their way out of a four-armed maze than individuals reared in standard, non-enriched hatchery conditions. The enrichment promoted neural plasticity in the telencephalon with a positive effect on later life. Cognitive abilities can also be improved by exposure to environmental change during early ontogeny (Kotrschal & Taborsky, 2010). Individuals of *S. pleurospilus* experiencing changed food rations early in life outperformed fish kept on constant rations in a later learning task. This difference in learning abilities between individuals remained constant between juvenile and adult stages of the same fish tested 1 year apart.

Environmental complexity and different kinds of sensory input can lead to neural developmental and plastic modifications; but if understimulated, fishes typically develop smaller brains (Mayer *et al.*, 2011). In salmonids, tank-rearing influences anatomical characteristics such as the development of the forebrain (telencephalon), cerebellum and optic tectum (Marchetti & Nevitt, 2003; Kihslinger & Nevitt, 2006; Kihslinger *et al.*, 2006). Cultured *Oncorhynchus* spp. have smaller brains, dendrite modifications of the dendritic structure and gene expression of neuroplasticity markers. Also, sensory organs, such as the lateral line system and eyes, may be modified and influence behavioural performance of hatchery fishes (Marchetti & Nevitt, 2003; Anras & Lagardere, 2004). Also, the brain gene expression profiles in *S. salar* are affected by rearing environments, such as hatchery and river, as well as between reproductive tactics independent of rearing environment (Aubin-Horth *et al.*, 2005). Important in the growth of the various regions of the brain are proliferation and incorporation of new neurons that handle new information. In *D. rerio*, habitat enrichment during early rearing increased proliferating cell nuclear antigen positive cells in the forebrain (von Krogh *et al.*, 2010), and in the weakly electric fish *Brachyhypopomus gauderio* Giora

& Malabarba 2009 from a natural environment had greater rates of brain cell prolif-
eration than conspecifics reared in social or isolated captive environments (Dunlap
et al., 2011).

Mate choice

Early experience may influence mate choice. In cross-fostering experiments with the
closely related cichlid species pair *Haplochromis pundamilia* (Seehausen & Bouton
1998) and *Haplochromis nyererei* Witte-Maas & Witte 1985 of Lake Victoria, Verzij-
den & Cate (2007) showed that young females develop a sexual preference for males
of their foster mothers' species. Crosses were made both ways and showed that these
species reversed their species assortative mating preferences when developed in the
mouth of a female of the other species. It is not known whether the colour or smell of
the foster mother were imprinted in the offspring, but obviously, this learning may be
important in the speciation process of the haplochromine cichlids of the species flocks
in the great African lakes.

Thus, a whole suite of behavioural reactions can be influenced by early experiences.
Since much of this research is very recent, it is expected that several more examples
will be published rapidly enhancing knowledge about behavioural effects of early expe-
riences.

FUTURE RESEARCH

Important future questions are to what degree parental and early environmental influ-
ences affect future performances of fishes and what the genetic, epigenetic, neural and
hormonal mechanisms are. For instance, environmental influences during embryogene-
sis may have effects on the adult phenotype that are difficult to realize when monitoring
performances of the organism in the field. Without this knowledge, present interpre-
tation of, for example, climate change effects may be skewed or wrong. Because of
the time lapse between cause and effect, effects of such early influences are chiefly
discovered through long-lasting experimental research.

The links between early influences, behaviour, growth and life-history character-
istics are still poorly developed, and new knowledge about these relationships will
be valuable for understanding of population and species effects in relation to natural
and anthropogenic habitat modifications and climate change (Fig. 1). Future research
may focus on genetic mechanisms influencing phenotypic plasticity caused by early
and trans-generational influences, and link effects of early influences and later norms
of reaction in life-history and behavioural traits. Arising questions are: (1) Is there
a relationship between boldness, the early behavioural syndrome linking activity to
aggressiveness and exploration tendency (Andriaenssens & Johnsson, 2013), migra-
tory tendency and epigenetics? (2) Does embryonic temperature or other environmental
stimuli influence later activity, boldness and social behaviour? (3) Is the tendency
to migrate in partly migratory populations influenced by epigenetics? (4) Are other
life-history characteristics influenced by environmental stimuli during embryogene-
sis? (5) To what degree is the phenology of species influenced by epigenetics? (6) To
what degree is later phenotypic response to early environmental influences inherited
and thereby influenced by natural selection (Walsh & Reznick, 2011)? (7) How is indi-
vidual fitness related to this phenotypic variability? (8) Is there a cost of phenotypic
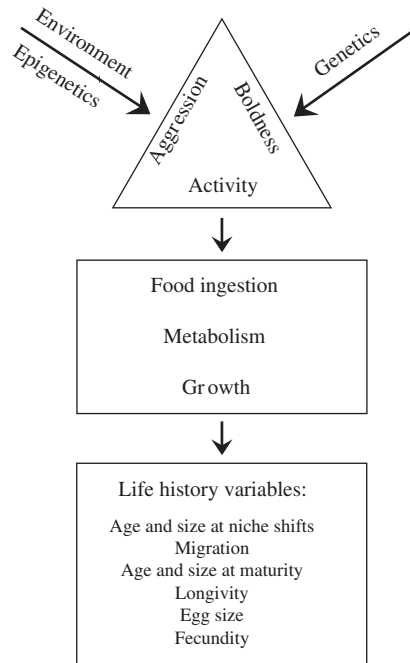
FIG. 1. Genetics and environment affect personality development, social behaviour and activity of fishes. The environmental effect may be partly epigenetic with likely effects on food consumption, metabolic rate and amount of surplus energy used for growth with subsequent effects on life-history traits.

flexibility? (9) Which epigenetic mechanisms are involved in phenotypically plastic reaction norms? (10) How are epigenetic effects conveyed to later activated life stages (neural, hormonal, enzymes)?

Moran & Pérez-Figueroa (2011) compare methylation patterns between mature and immature parr of *S. salar* from two different rivers in order to infer if DNA methylation differences may be related to their maturation condition. Contrary to mature parr, immature parr migrate to the ocean and become large fish before they attain maturity. Their results revealed that genetically similar mature and immature salmon parr present high levels of DNA methylation variation in two of the three analysed tissues (liver, brain and gonads), and hypothesized that early maturation may be mediated mostly by epigenetic processes rather than by genetic differences between the young fish as suggested by Piché *et al.* (2008). If there is an epigenetic relationship between migratory tendency and environmental influence during embryogenesis, this may explain the finding of Giger *et al.* (2006) that there is no apparent inherited genetic difference between resident and migratory *S. trutta*, but a difference exists in their gene expressions. Life-history characteristics are quantitative traits influenced by a large number of genes, whereas the expression may be determined by a few control genes under strong environmental influence. Also, there may be density-dependent influence conveyed during early juvenile stages related to growth, metabolic rate or degree of lipid reserve energy at that time (Jonsson & Jonsson, 1993; Olsson *et al.*, 2006), but neither epigenetic nor density-dependent influences on migration in partly migratory populations have been studied very much.

Early environmental effects on later performance in fishes are as yet a poorly developed field. New studies should be aimed at exploiting the mechanisms of this plasticity, and how the norms of reaction are and reflect differences in ability of the fishes to respond to environmental change. By increasing the understanding of interactions between environments and genotypes, the capacity to predict population responses to early influences on later phenotypic plasticity will be refined. Evidence indicates that the degree of plasticity is heritable and that population differences reflect adaptive responses formed by natural selection to local environments. In evolutionary ecology and conservation biology, it is important to understand how these vary within populations across environmental gradients, among populations and among species. Such knowledge may influence evaluation of ecological responses observed across environmental gradients.

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