Why do some fish grow faster than others?

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Abstract

All animals must acquire food to grow, but there is a vast diversity in how different species and even different individuals approach and achieve this task. Individuals within a species appear to fall along a bold-shy continuum, whereby some fish acquire food aggressively and with seemingly high risk, while others appear more submissive and opportunistic. Greater food consumption generally results in faster growth, but only if the energy acquired through food is more than enough to compensate for heightened metabolism associated with a more active lifestyle. Fast-growing phenotypes also tend to have elevated baseline metabolism – at least when food is plentiful – which may be linked with gut morphology and digestive efficiency. The net energy gained from a meal (as calculated from the specific dynamic action (SDA) coefficient) is optimised with larger meal sizes, but the digestion of large meals can erode the aerobic metabolic scope available for other critical activities such as predator avoidance, perhaps at an interindividual level. Thus, complex interactions between an individual's genes and environment are likely to regulate the growth phenotype. This review compiles available knowledge to shed light on the question: Why do some fish grow faster than others? We discuss the elaborate interrelationships between behaviour, physiology and the gut microbiome with a goal to better understand what drives intraspecific differences in growth performance.

Key words: behaviour, digestion, growth, gut microbiome, intraspecific, interindividual, metabolism, phenotype, performance

1. Introduction

Growth is arguably the most important determinant for the survival of most organisms, perhaps especially aquatic ectotherms like fishes where growth is particularly plastic and early-life mortality can be extreme (Peters & Peters, 1986; Clark *et al.*, 2016; Goatley & Bellwood, 2016). In a fish's early life stages, survival depends on the ability of an individual to avoid predation and compete for resources like space and food. Indeed, many species are known to cannibalise conspecific individuals as they outgrow them (Duk *et al.*, 2017). Thus, an individual is much more likely to succeed and become established if it grows big and does so quickly (Stige *et al.*, 2019). Despite this, wide discrepancies in growth and feed intake among closely related individuals are common in fish populations (Carter *et al.*, 1992; Pfister & Stevens, 2003; Vincenzi *et al.*, 2014). Even when genetic diversity is minimised (e.g., siblings) and individuals are reared in the same environment with surplus food, some fish grow faster and bigger (Table 1).

In addition to the importance of growth phenotypes in shaping ecological communities, the applied importance is widespread. For example, fisheries sectors often harvest based on fish size (Darimont *et al.*, 2009; Sutter *et al.*, 2012; Uusi-Heikkilä *et al.*, 2015). In aquaculture, fast-growing phenotypes are able to achieve target sizes sooner to reduce production costs and resource use (Asche, 2008; Kumar & Engle, 2016). In fish stocking programs, whether for conservation or recreational angling purposes, the release of fast-growing juvenile fish may minimise predation mortality to enhance survival and reduce the time taken to achieve target adult sizes for spawning or capture (Hutchison *et al.*, 2012; Barrow *et al.*, 2021).

Living in the current era of climate change, there is also much interest in understanding which genotypes and phenotypes may help to future-proof animal populations and associated industries (Somero, 2010; Seebacher, White & Franklin, 2015; Morgan *et al.*, 2022). It is not known whether the fast-growing phenotypes in today's climate will be the fast-growing phenotypes of future climates, or whether interindividual rankings will reorder as environmental conditions change.

Filling these gaps requires an understanding of the drivers of phenotypic growth variation in fish, yet to our knowledge, there has been no previous attempt to compile the mechanisms underlying interindividual differences in fish growth. No doubt, the development of a beneficial growth phenotype will depend on complex interactions between a range of determining factors. This review presents a summary of current knowledge on interindividual growth differences within fish populations. We draw on examples from lab- and field-based studies to identify potential drivers of this phenotypic diversity, and provide future directions to help guide research in this field.

2. Parental influences

The growth phenotype of an individual will be influenced by its own environment and potentially the environment experienced by its parents (Monaghan, 2008). For instance, environmental factors that affect maternal fitness will influence maternal investment into individual offspring and the emergence and diversity of early life phenotypes (Burton & Metcalfe, 2014; Van Leeuwen *et al.*, 2016; Feiner *et al.*, 2016; Cortese *et al.*, 2022). Parental temperature (Colson *et al.*, 2019; Chang, Lee & Munch, 2021), oxygen (Ho & Burggren, 2012), stress (Eriksen *et al.*, 2006, 2007, 2011), social ranking or interactions with conspecifics (Burton *et al.*, 2013) can all influence egg size and/or composition to modulate offspring growth, survival and even behaviour. Variation in egg size both between females and within the same clutch has been reported in salmonids (Beacham & Murray, 1987, 1993; Einum, 2003; Self *et al.*, 2018). It is generally assumed that larger eggs give rise to an individual with a competitive size advantage (Einum & Fleming, 1999; Thorn & Morbey, 2018). In brown trout (*Salmo trutta*), individuals hatched from larger eggs had growth and survival advantages over individuals hatched from smaller eggs (Einum & Fleming, 1999). However, other studies on the same species have found higher rates of survival in individuals hatching from small eggs as opposed to large eggs (Régnier *et al.*, 2013). Likewise, in steelhead trout (*Oncorhynchus mykiss*), smaller eggs hatched sooner and had higher growth rates than fish from larger eggs (Self *et al.*, 2018). Both within- and between-clutch variation in offspring phenotypes, like egg size and larval growth, are known to increase in more variable or unpredictable environments (Crean & Marshall, 2009). This adaptive phenotypic response to environmental heterogeneity is an example of ‘bet hedging’ and allows mothers to adjust the phenotype of sibling offspring to increase variability and improve fitness and survival of at least some of the clutch (Mousseau & Fox, 1998; Crean & Marshall, 2009). In some salmonid species or populations, egg size remains consistent within a clutch, suggesting sibling survival or growth could be related to the distribution of phenotypes within an egg mass before spawning (Burton *et al.*, 2013).

The maternal endocrine system is closely associated with its progeny and will at least partly drive phenotypic differences between siblings (Eriksen *et al.*, 2007; Sopinka *et al.*, 2017). Maternal hormones are accumulated and absorbed into the nutritive yolk sac of developing embryos during oogenesis (Hwang *et al.*, 1992; Mylonas, Sullivan & Hinshaw, 1994; Schreck, Contreras-Sanchez & Fitzpatrick, 2001; Eriksen *et al.*, 2007, 2011; Sopinka *et al.*, 2017). In fact, the developmental, reproductive and metabolic hormones present in the yolk sac of developing embryos occur in similar quantities to that of maternal blood plasma (Hwang *et al.*, 1992; Mylonas *et al.*, 1994; Schreck *et al.*, 2001). An example of this relationship is seen in a consistency of hormone patterns between stressed mothers and their offspring (Eriksen *et al.*, 2011). Given that growth suppression in teleost fish is a consequence of most forms of environmental stress (Pickering, 1990, 1993), maternal stressor exposure activates the transmission of the stress response, binding circulating cortisol in target tissues and developing follicles in the female's ovaries (Sopinka *et al.*, 2017). Some studies suggest that paternal effects will also influence the endocrine state of offspring (McGhee & Bell, 2014; Hellmann, Carlson & Bell, 2021). Paternal predation exposure of threespined sticklebacks (*Gasterosteus aculeatus*) reduced activity and elevated cortisol concentrations in offspring (Hellmann *et al.*, 2021). Parental experiences of stress can therefore expose the developing embryos to elevated concentrations of glucocorticoids, which may impact subsequent growth at an individual level.

Experimentally manipulating the maternal endocrine state of female Atlantic salmon (*Salmo salar*) with cortisol led to offspring that grew less efficiently, had reduced survival and higher incidences of malformation compared with half-sib offspring from mothers with no cortisol treatment (Eriksen *et al.*, 2006, 2007, 2011). In some species, like the Atlantic halibut (*Hippoglossus hippoglossus*), differences in egg cortisol have no influence on offspring phenotypes like larval size (Skaalsvik *et al.*, 2015). As well, differential impacts of egg cortisol exist between wild fish populations and populations reared in laboratory environments (Gingerich & Suski, 2011). Variation in total egg cortisol concentration also exists between individuals from the same clutch (i.e., between full sibs) (Sopinka *et al.*, 2017). Previous research suggests that intra-female variation in egg cortisol of brown trout will depend on the position of eggs within the ovary (anterior, middle, and posterior) (Suter, 2002). Interestingly, other studies have reported that location in the egg mass affects social dominance, behavioural phenotypes and egg size in resulting juveniles of the same species (Burton *et al.*, 2013). Taken together, independent of egg size differences, there may be a role of egg positioning within the clutch in determining the growth rates of early life stages.

3. Stress and the social environment

Stress hormones like catecholamines and cortisol function to mobilise energy reserves that help fish to escape, avoid or overcome an immediate threat (Bonga, 1997). Fish experiencing stress will divert resources like oxygen and energy away from investment activities (e.g., growth and reproduction) and toward activities like tissue repair (Bonga, 1997). As a result, the performance capacity of fish during stress can be compromised (Madison *et al.*, 2015). Maintenance of plasma cortisol at 116 ng/ml via implant micro-pumps in rainbow trout led to a 60% reduction in feed intake and up to 80% reduction in mass gain (Madison *et al.*, 2015). However, growth responses to stressors can vary. For example, in threespined stickleback (*Gasterosteus aculeatus*), early exposure to a predation risk increased juvenile somatic growth, but caused a decrease in size at adulthood (Bell *et al.*, 2011). In fish and other vertebrates, the stress response is initiated and controlled by the activation of the hypothalamic-pituitary-interrenal/adrenal (HPI or HPA) axis (Bonga, 1997; Bernier & Peter, 2001; Gilmour, Dibattista & Thomas, 2005). The HPI or HPA axis describes the communication that is present between the hypothalamus and the pituitary gland in the fish brain and the head kidney (Bonga, 1997; Bernier & Peter, 2001). When exposed to a stressor, the hypothalamus releases corticotropin-releasing factor/hormone (CRF or CRH), which stimulates the release of adrenocorticotropic hormone (ACTH) from the pituitary (Bernier & Peter, 2001). ACTH binds to receptors on the interrenal cells in the head kidney, initiating a biochemical cascade that results in the synthesis of cortisol (Bernier & Peter, 2001). Anthropogenic stressors have also been shown to disrupt the thyroid and alter levels of thyroid hormones (TH) in fishes (Deal & Volkoff, 2020; Besson *et al.*, 2020). Thyroid hormones are critical to early fish development, behaviour (Besson *et al.*, 2020) and the regulation of somatic growth and appetite (e.g., through the hypothalamic-pituitary-somatotropic (HPS) axis) (Deal & Volkoff, 2020). Wild and captive fish can face a multitude of stressors that all have the potential to induce chronic stress (i.e., sustained, elevated plasma glucocorticoids), and inhibit growth through impacts on the metabolic, digestive and behavioural phenotype (Bonga, 1997; Mommsen, Vijayan & Moon, 1999; Barton, 2002; Deal & Volkoff, 2020).

Stressful social interactions (or complete lack of social stimuli) between conspecifics can lead to a stress response that controls behaviours like aggression, appetite, foraging and locomotion (Gilmour *et al.*, 2005). These behaviours are often associated with descriptive terms for individuals like ‘bold’, ‘shy’, ‘dominant’ or ‘subordinate’ (Gilmour *et al.*, 2005; Metcalfe, Van Leeuwen & Killen, 2016). These ‘behavioural phenotypes’ may shift through time and change with the social environment and with resources like food availability, shelter and habitat (Wieser, Krumschnabel & Ojwang-Okwor, 1992; Hofmann, Benson & Fernald, 1999; Höjesjö, Johnsson & Bohlin, 2004; Reid, Armstrong & Metcalfe, 2012). As a result, in some species, subordinate fish show suppression in appetite, feed intake, aggression, locomotion and growth (Gilmour *et al.*, 2005), while dominant individuals have opposing behaviours that allow them to monopolise resources and gain a competitive growth advantage (Abbott & Dill, 1989; Metcalfe, Wright & Thorpe, 1992). In subordinate European eels (*Anguilla anguilla*), social dominance acted as a significant stressor causing reduced feed intake, growth, extensive intestinal lesions and a reduced stomach size (Peters, 1982). When dominant and subordinate salmonids were confined in pairs, an antagonistic interaction caused a rapid increase in plasma cortisol in both fish (Øverli, Harris & Winberg, 1999a), yet the blood cortisol concentration of the dominant individual returned to resting levels much quicker (within 3 h; Øverli *et al.*, 1999a) than the subordinate individual (up to 7 days; Øverli *et al.*, 1999a; Sloman *et al.*, 2001). Thus, in salmonids, social subordination is viewed as a chronic stressor, which causes a chronic activation of the HPI axis, regulating subordinate traits like appetite to affect grow rates (Øverli *et al.*, 1999b, 1999a; Gilmour *et al.*, 2005).

Differences in group size (Carter *et al.*, 1992) or environment (Höjesjö *et al.*, 2004), as well as species differences in social structure (Hofmann *et al.*, 1999) will all contribute to differences in the relationships between growth, dominance and stress. For example, while subordinate salmonids often have higher plasma cortisol levels (Laidley & Leatherland, 1988; Pottinger & Pickering, 1992; Øverli *et al.*, 1999a; Sloman *et al.*, 2000, 2001; Elofsson *et al.*, 2000; Pottinger & Carrick, 2001; Höglund, Balm & Winberg, 2002), in small groups behavioural responses to cortisol vary. Some studies report elevated cortisol levels in subordinate fish (Ejike & Schreck, 1980; Winberg & Lepage, 1998; Höglund, Balm & Winberg, 2000), while others do not (Pottinger & Pickering, 1992; Øverli *et al.*, 1999b; Sloman *et al.*, 2000, 2001).

In the African cichlid fish, *Haplochromis burtoni*, only territorial males (i.e., dominant individuals) are reproductively active (Hofmann *et al.*, 1999). The territorial males will work to maintain territories and court females, while non-territorial males (i.e., subordinate individuals) are sexually regressed and school with females (Fernald & Hirata, 1977). Because of reduced energy expenditure, non-territorial males and animals ascending in social rank have higher rates of somatic growth (Hofmann *et al.*, 1999). Social status is highly flexible in *H. burtoni* and as a result the growth rates of individuals change frequently within a population (Hofmann *et al.*, 1999). Reversible phenotypic plasticity is a crucial life-history trait that is thought to enable this species to shift resources from reproduction to growth and vice versa (Hofmann *et al.*, 1999; Trainor & Hofmann, 2007; Dijkstra *et al.*, 2017). The shifts in social dominance and growth of *H. burtoni* are thought to be regulated by multiple endocrine pathways and involve gonadotropin-releasing hormone (GnRH), somatostatin and the melanocortin system (Hofmann *et al.*, 1999; Trainor & Hofmann, 2007; Dijkstra *et al.*, 2017). In other cichlid species (*Lamprologus callipterus*), males within a population can adopt different reproductive strategies that lead to multiple growth patterns and the presence of both small ‘dwarfed’ and large ‘nested’ males of the same age within the same population (Wirtz-Ocaňa *et al.*, 2013). The endocrine profiles of these species, and those that show clear sex-specific size dimorphism (Pietsch, 1976; Isakov, 2022) could provide useful insight into the drivers of interindividual growth differences (Malison *et al.*, 1985, 1988).

In social species where social dominance determines appetite and access to food and resources, behavioural phenotypes and stress will play an important role in the development of multiple growth phenotypes within a population. However, in schooling, non-social or non-aggressive species, where social dominance is not considered to be a significant factor, interindividual differences in growth can still exist (Cui & Liu, 1990; Carter *et al.*, 1992). Similarly, in lab-based studies, where social interactions are removed (e.g., through isolation in individual tanks), obvious growth differences persist (Norin, Malte & Clark, 2016). In the above cases, grow rates are unlikely to be regulated by social stress, and therefore metabolic and digestive phenotypes may play a role.

4. The metabolic phenotype

The metabolic phenotype shapes an animal’s energy budget and will dictate the energy spent by an animal at rest, during digestion and during routine or maximum activity (Clark, Sandblom & Jutfelt, 2013). Large individual variations in the standard metabolic rate (SMR), routine metabolic rate (RMR, metabolic rate at regular activity levels), maximum metabolic rate (MMR), specific dynamic action (SDA, energy cost of digestion) and aerobic scope (aka ‘scope for activity’) are common in fish populations (Metcalfe *et al.*, 2016). Between individuals of the same species there can be a 2-3-fold variation in SMR and MMR (Rice, 1990). Such differences in energy allocation and use between individuals will influence the capacity to convert food energy into tissues for subsequent growth.

Under ad-libitum feeding conditions we expect faster growers to have a higher SMR than their slow-growing conspecifics (Norin & Malte, 2012; Norin & Clark, 2017) (Fig. 1). Previous research on barramundi (*Lates calcarifer*) has shown that SMR is positively correlated with specific growth rate (SGR) (Norin *et al.*, 2016). Norin et al (2016) found that individuals with a high SMR ate more food and grew quicker than conspecifics with a low SMR. That is, high SMR individuals consumed a surplus of food to more than compensate for their higher baseline metabolic requirements (Norin *et al.*, 2016). In social species, high SMR individuals tend to display a dominant behavioural phenotype that drives behaviours allowing them to monopolise resources, consume more food and grow bigger (Reid *et al.*, 2012; Hoogenboom *et al.*, 2013; Metcalfe *et al.*, 2016). This competitive growth advantage among high SMR fishes is thought to be modulated by environmental conditions like food supply (Burton *et al.*, 2011), feeding conditions (Killen, Marras & McKenzie, 2011; Metcalfe *et al.*, 2016) and habitat complexity (Robertsen *et al.*, 2014). When food is restricted, the relative growth rate of high SMR individuals may be less than their low SMR conspecifics (O'Connor, Taylor & Metcalfe, 2000; Norin & Malte, 2011). While there is evidence of a link between high SMR individuals and growth when food is abundant, this relationship does not persist across all species or life stages. In larval Atlantic herring (*Clupea harengus*; 7 days post-hatch), interindividual differences in SMR were not associated with growth (Moyano *et al.*, 2017). There is some evidence that observed links between metabolism and growth may be related to interindividual variation in the efficiency with which substrates are converted into ATP at the mitochondria (e.g., via 'proton leak'; Salin *et al.*, 2019). Additionally, the metabolic traits of individuals respond differently to environmental challenges (Norin *et al.*, 2016), suggesting that the relative ranking of slow- and fast-growing individuals may change across days, seasons, and with climate change.

In the context of the metabolic phenotype, we might expect that individuals with large relative organ masses would exhibit proportionally greater metabolic rate with potential implications for growth (Ferrell, 1988; Piersma & Lindström, 1997). However, in brown trout (*Salmo trutta*), no relationship between SMR, MMR and the residual size (mass) of metabolically active internal organs (stomach, intestine, liver, heart, spleen) was found (Norin & Malte, 2012). Instead, this study found that the SMR, MMR and aerobic scope were significantly correlated with liver activity of the aerobic mitochondrial enzyme, cytochrome c-oxidase. The study concluded that intraspecific variation in the metabolic rate of fish can be found at a lower organisational level than organ size alone (Norin & Malte, 2012). Thus, while it appears that there is no clear link between relative organ size, metabolism and growth, more research is required to understand the relationships between these parameters.

Variation in the energy cost of digestion, SDA, is also thought to be correlated with SMR (Secor, 2009). The SDA accounts for the energy expended on every physiological, mechanical and biochemical process that facilitates the breakdown of food, and the absorption, transport, and assimilation of its nutrients (Secor, 2017). Fish with a higher SMR can exhibit a higher

SDA peak (i.e., peak in oxygen consumption is higher during digestion), but shorter SDA duration (i.e., digestion finishes sooner), meaning high SMR individuals can have faster digestion rates and potentially faster growth (Metcalfe *et al.*, 2016). Juvenile Atlantic salmon (*Salmo salar*) with a high SMR had a greater (more energetically expensive) SDA, but a shorter SDA duration than those with a low SMR phenotype (Millidine, Armstrong & Metcalfe, 2009). Thus, despite having a greater baseline energy expenditure, salmon with a high SMR have a shorter SDA duration and can therefore feed more frequently to facilitate faster growth (Millidine *et al.*, 2009).

Similarly, the SDA is also associated with and governed by the available aerobic scope and postprandial residual aerobic scope (PRAS) of an individual (Jutfelt *et al.*, 2021) (Fig. 1). The aerobic scope describes the scope for activity and is calculated as the difference between MMR and SMR (Clark *et al.*, 2013). PRAS describes the scope for activity on top of digestion and is calculated as the difference between the peak of the SDA and MMR (Jutfelt *et al.*, 2021). In less athletic species that prioritise feeding over movement, the scope for activity can be defined as the difference between the active metabolic rate (AMR) and SMR (Steell *et al.*, 2019). The SDA can take up a significant proportion of the aerobic scope during digestion in fish (e.g., up to 77% in barramundi (*Lates calcarifer*); Norin & Clark, 2017). Moreover, in the lionfish (*Pterois spp.*), the maximum metabolic rate during digestion (SDA peak) can exceed the metabolic rate reached following exhaustive exercise (Steell *et al.*, 2019). In some species, environmental conditions like elevated temperatures can temporally compress the SDA, further constraining aerobic scope and PRAS and driving a reduction in feed intake (Jordan & Steffensen, 2007; Oliver *et al.*, 2017; Wade *et al.*, 2019; Jutfelt *et al.*, 2021). Since the SDA increases with meal size to occupy more of the available aerobic scope (Fu, Xie & Cao, 2005; Jordan & Steffensen, 2007; Secor, 2009), modulating feed intake during warming is hypothesised to ‘protect’ PRAS and maximise the energy available for activities outside of digestion, like swimming and avoiding predation (Jutfelt *et al.*, 2021). This hypothesis would suggest that in benign environments, individuals with a greater MMR (and therefore greater PRAS) may be able to maximise energy gains and growth by consuming more food relative to low MMR/PRAS individuals (Fig. 1). Conversely, recent work in sham-fed Chinook salmon (*Oncorhynchus tshawytscha*) showed that elevated temperature had no effect on PRAS during the digestion of a 2% meal ration (Lo *et al.*, 2022). Contrary to the hypothesis presented by Jutfelt *et al* (2021), some species may not mediate food intake based on the occupation of the

SDA in their scope for activity and in turn feed intake and growth may not be limited by phenotypic differences in AMR, SMR or MMR for those species.

The SDA coefficient (% of meal energy used in the SDA) typically ranges 5-20% in fish (Beamish, 1974; Fu *et al.*, 2005; Secor, 2009), but can reach up to 50% in some fish species (Secor, 2017). It is generally assumed that a larger SDA coefficient for a given meal size is indicative of inefficient digestion and less absorbed energy available for growth. Therefore, if environmental and nutritional requirements remain constant, individuals with a smaller SDA coefficient should grow more efficiently than individuals with a larger SDA coefficient (Jobling, 1994; Secor, 2009). Recently tested in a study on juvenile barramundi (*Lates calcarifer*), Goodrich *et al.*, (2021) showed that reducing the SDA coefficient through dietary acidification can lead to acute improvements in fish growth efficiency, but these improvements declined over time.

In contrast, Carter and Brafield (1992) reported a positive relationship between the SDA and the specific growth rate of grass carp (*Ctenopharyngodon idella*). These findings contradict the original theory presented by Jobling (1994) and Secor (2009) and suggest that the SDA coefficient may also be indicative of digestive capacity and not just energy expenditure. For example, a larger SDA coefficient may indicate greater capacity for energetically expensive processes like protein synthesis. Protein synthesis uses four ATPs to bind one amino acid to the next, and for this reason is known to be a primary contributor to the SDA (Lusk, 1922; Jobling, 1985; Brown & Cameron, 1991a, 1991b). The total energetic cost to synthesise 1 gram of protein has been estimated to equal ~50 mmol of ATP equivalents (Reeds, Fuller & Nicholson, 1985). Infusion of an amino acid mixture directly into the blood stream of fasted channel catfish (*Ictalurus punctatus*) was able to elicit an SDA response and significantly increase oxygen consumption above resting levels (Brown & Cameron, 1991a). In cod (*Gadus morhua*), protein synthesis is thought to contribute between 20 to 40% of the SDA (Lyndon, Houlihan & Hall, 1992; Smith & Houlihan, 1995). Therefore, while a larger SDA may indicate greater energetic costs, it may also indicate greater capacity to assimilate nutrients from food for subsequent growth. In these instances, individuals with a beneficial SDA phenotype (e.g., high SDA coefficient) may have a competitive growth advantage over conspecifics with a reduced SDA phenotype (e.g., low SDA coefficient), at least when food is abundant (Fig. 1).

5. The digestive phenotype

Phenotypic flexibility is well documented in the digestive systems of reptiles (Secor, Stein & Diamond, 1994; Secor & Diamond, 2000), birds (McWilliams & Karasov, 2001), mammals (Naya et al., 2007), and fishes (Armstrong & Bond, 2013; Blier et al., 2007; Htun-Han, 1978; Jobling et al., 1998; Piersma & Gils, 2011; Piersma & Lindström, 1997). Digestive tract adjustments, like changing organ size or length (Bergot, Blanc & Escaffre, 1981) and rates of protein synthesis, retention and degradation (Carter & Houlihan, 2001), are often associated with the amount of nutrients and energy that fish consume and assimilate. A multitude of studies have shown that the response of the digestive tract will vary with the intensity of the energetic demand imposed on the animal (Naya *et al.*, 2007), the frequency of feeding in nature (Secor & Diamond, 2000; Secor, 2005a, 2005b), the time to and type of first feed consumed by fish larvae (Kolkovski, 2001; Ching *et al.*, 2016), the environmental conditions experienced by different populations of the same species (Kristan & Hammond, 2003; Bacigalupe *et al.*, 2004; Tracy & Diamond, 2005), and the level of environmental variability under which different species have evolved (Naya, Bozinovic & Karasov, 2008). When fed ad libitum and reared in the same environmental conditions, phenotypic changes that result in an increase in the functional capacity of the digestive system are likely to lead to better performance and interindividual differences in fish growth.

Proteins from ingested food are central to animal growth and tissue maintenance. Proteins are incorporated into new tissue for growth through processes like protein cycling (Smith & Houlihan, 1995; Carter & Houlihan, 2001). Growth rates in fish will be controlled by the balance between rates of protein synthesis, retention and degradation (Houlihan *et al.*, 1988; Houlihan, Hall & Gray, 1989; Carter *et al.*, 1993a). In grass carp (*Ctenopharyngodon idella*), faster growing individuals had a lower RNA to protein ratio (capacity for protein synthesis), variable rates of protein synthesis, yet higher retention of synthesized protein, higher RNA activity and lower rates of protein degradation (Carter *et al.*, 1993a). In Atlantic salmon (*Salmo salar*), individual variation in growth efficiency was related to differences in protein retention efficiency but no difference in the capacity for protein synthesis (Carter *et al.*, 1993b). Similarly, more efficient, faster growing rainbow trout (*Oncorhynchus mykiss*) had reduced rates of protein degradation in comparison to their slower growing conspecifics (McCarthy, Houlihan & Carter, 1994).

In the wild, some fish species adaptively regulate digestive capacity to match ambient levels of demand (Kent, Prosser & Graham, 1992; Jobling *et al.*, 1998; Armstrong & Bond, 2013;

Furey *et al.*, 2016). In their natural streams, Dolly Varden trout (*Salvelinus malma*) take advantage of annual resource pulses that occur as a result of the spawning migration of Pacific salmon. During a small 5-week period where Pacific salmon spawn, Dolly Varden maximise energy gain by significantly increasing gut size to gorge on the eggs of Pacific salmon (Armstrong & Bond, 2013). Similarly, binge-feeding (hyperphagia) in bull trout (*Salvelinus confluentus*) during a prey pulse of out-migrating juvenile sockeye salmon (*Oncorhynchus nerka*) was facilitated by an increase in gut volume (Furey *et al.*, 2016). Outside of resource pulses, fishes adopt a significantly smaller, and less energetically expensive gut (Armstrong & Bond, 2013). Alternating periods of feast and famine could generate trade-offs between phenotypes that maximize energy gain during resource abundance, and those that conserve energy during resource scarcity (Gans, 1979; Diamond, 2002; Piersma & Gils, 2011; Armstrong & Schindler, 2011; Armstrong & Bond, 2013). When reared in the same environment and fed in a food surplus, we would therefore expect that individuals with a larger and more expensive gut would maximise the energy gained from ingested food. The greater energetic cost of a large gut, provide some explanation for why some individuals have proportionally higher SDA and higher growth rates.

Despite the above possibilities, few studies have assessed the relationship between interindividual differences in gut size/anatomy, and variation in fish growth or appetite. Some evidence suggests that full siblings with a greater number of pyloric caeca in the digestive tract grow larger and are bigger than individuals of the same age (Bergot *et al.*, 1981). The pyloric caeca are an important digestive organ responsible for the uptake of nutrients from food in some fish species (Buddington & Diamond, 1986). Possessing a larger number of caeca would be advantageous in a benign environment where all individuals have unlimited access to resources. Indeed, research on the cichlid fish (*Simochromis pleurospilus*) found that plasticity in digestive efficiency and growth was facilitated by possessing heavier digestive organs, yet dependent on early-life food availability (Kotrschal, Szidat & Taborsky, 2014). *S. pleurospilus* that were kept at a constant higher ration grew considerably faster than conspecifics offered lower food rations. However, *S. pleurospilus* fed a lower food ration were able to buffer the negative growth impacts by developing significantly heavier digestive organs, which made them more efficient at digesting food as adults. This suggests that digestive efficiency is influenced by food availability, growth and feed intake during a narrow ‘plasticity window’ that occurs in a fish’s juvenile stages (Kotrschal *et al.*, 2014). Individuals reared in the same food-limited environment may therefore adjust their gut for either immediate or delayed growth benefits (e.g., reducing organ size to maintain energy efficiency in a low-food juvenile environment, or increasing organ size to maximise energy gain in a future high-food adult environment) leading to differential juvenile and adult growth phenotypes.

Similarly, other early developmental characteristics like the time to first feed can influence the functional capacity of the digestive system in fish larvae to affect early grow rates and survival. In larval tiger grouper (*Epinephelus fuscoguttatus*), delaying first feeding to 6 h after mouth opening resulted in an almost 50 % reduction in the height of the gut epithelium, causing delays in fish development and reduced growth (Ching *et al.*, 2016). The type of food a larval fish first eats can also play a significant role in the capacity of their gastrointestinal tract. Most larval fish lack fully functioning digestive systems for the first weeks after hatching (Dabrowski, 1984). It has been proposed that larvae utilise the digestive enzymes present in their prey to facilitate the process of digestion until the larval alimentary system is fully developed (Dabrowski, 1984; Lauff & Hofer, 1984; Kolkovski *et al.*, 1993; Kolkovski, 2001). Support for this theory is mixed, with some studies reporting as much as 40 – 80% of larval enzymatic activity is 'donated' by live food organisms (Dabrowski & Glogowski, 1977a, 1977b), and others suggesting live food contribution to direct digestive enzymes is negligible (Zambonino-Infante *et al.*, 1996; Cahu & Zambonino-Infante, 1997). However, live feeds also contain gut neuropeptides and other nutritional growth factors that are known to enhance digestive capacity (Kolkovski, 2001). This may at least partly explain the improved grow rates observed in marine fish larvae reared on live foods as opposed to formulated micro diets (Kolkovski, 2001, 2013; Giebichenstein *et al.*, 2022). Variation in early developmental characteristics like the time to and type of first feed consumed by individual fish larvae could therefore contribute to differences in digestive efficiency, early growth phenotypes and interindividual fish growth within a population.

6. The gut microbiome

The community of microbes that colonise the gut of living animals (the gut microbiome) play an important functional role in almost every aspect of an animal's physiology (Tarnecki *et al.*, 2017). Previous research has found that the gut microbiome can affect host metabolism, nutrient absorption, behaviour, satiety, reproduction, development, the immune response and growth (Avella *et al.*, 2012; Carnevali, Avella & Gioacchini, 2013; Mayer, Tillisch & Gupta, 2015; Ghanbari, Kneifel & Domig, 2015; Wang *et al.*, 2018; Johnson & Foster, 2018; Perry *et al.*, 2020). In wild fish, microorganisms from food and the surrounding water adhere to and colonise the gut (Ghanbari *et al.*, 2015). The function of the gut microbiota and the physiological response of the host will depend on the composition of the microbes present in the intestines of the individual (Tarnecki *et al.*, 2017; Talwar *et al.*, 2018). Factors like age, species, diet, social status, developmental stage, geographical location, sex and environmental conditions like temperature, salinity and pH can all influence the type, diversity and abundance of gut microbes in fishes (Ringø *et al.*, 1997, 2016; Nayak, 2010; Bevins & Salzman, 2011; Li *et al.*, 2012, 2014; Ni *et al.*, 2014; Borrelli *et al.*, 2016).

Differences in growth have been associated with differences in the resident gut microbiota of carp (*Cyprinus carpio*) (Yanbo & Zirong, 2006; Li *et al.*, 2013), Nile tilapia (*Oreochromis* niloticus) (Elsabagh *et al.*, 2018; Deng *et al.*, 2021), rohu (*Labeo rohitaI*) (Ghosh, Sen & Ray, 2003; Ramachandran & Ray, 2007), European sea bass (*Dicentrarchus labrax*) (Carnevali *et al.*, 2006), zebrafish (*Danio rerio*) (Falcinelli *et al.*, 2015), Japanese flounder (*Paralichthys olivaceus*) (Ye *et al.*, 2011), rainbow trout (*Oncorhynchus mykiss*) (Ramos *et al.*, 2013; Khodadadi *et al.*, 2018) and Malaysian mahseer (*Tor tambroides*) (Asaduzzaman *et al.*, 2018). Some resident gut microbes are known to produce exogenous digestive enzymes and essential growth metabolites that aid fish digestion and nutrient assimilation to influence growth (Ray, Ghosh & Ringø, 2012; Semova *et al.*, 2012; Clements *et al.*, 2014). In fact, the absence of gut microbes, as in studies with germ-free zebrafish (*Danio rerio*), can inhibit the uptake of important nutrients like protein at the intestine (Bates *et al.*, 2006). The type, quantity, diversity and functional role of an individual's resident gut microbes could therefore contribute to the expression of plastic developmental phenotypes like growth. The possibility to improve growth outcomes with beneficial bacteria has led to a boom in research that aims to assess the application of probiotics to animal production systems, including aquaculture (Wang, Li & Lin, 2008; Perry *et al.*, 2020).

Targeted manipulation of the fish microbiome is reported to alter gut morphology (Elsabagh *et al.*, 2018), improve digestion and lipid metabolism (Falcinelli *et al.*, 2015), influence satiety and appetite (Falcinelli *et al.*, 2016; Gioacchini *et al.*, 2018), improve fish memory and even influence shoaling behaviours in zebrafish (Borrelli *et al.*, 2016; Zang *et al.*, 2019). Zebrafish fed the probiotic *Lactobacillus rhamnosus* for 8 days expressed a significant downregulation of appetite-stimulating (orexigenic) genes and a simultaneous upregulation of appetite-suppressing (anorexigenic) genes (Falcinelli *et al.*, 2016). These changes in gene expression were associated with differences in appetite and body glucose level between probiotic-fed fish and controls (Falcinelli *et al.*, 2016). Similarly, Malaysian mahseer (*Tor tambroides*), fed *Alcaligenes* sp. and *Bacillus* sp., were able to enhance growth by upregulating the growth-related genes, growth hormone (GH) and hepatic insulin-like growth factor IGF-1 (Asaduzzaman *et al.*, 2018). These results indicate that gut microbiota can regulate metabolic pathways that modulate the physiological state of hunger and satiety to influence feed intake and/or growth and also provide evidence of a gut-brain interaction previously only described in higher vertebrates (Mayer *et al.*, 2015; Butt & Volkoff, 2019).

The gut microbiota–brain axis describes the bi-directional communication that occurs between the gastrointestinal tract and the brain to influence host physiology and homeostasis (Mayer *et al.*, 2015; Butt & Volkoff, 2019). It is thought that gut microbiota release metabolites that act either directly on the brain or indirectly through the enteroendocrine cells of the gastrointestinal tract (Butt & Volkoff, 2019). Here, metabolites function to alter neuropeptide release to modulate the feeding behaviours and energy homeostasis of the host (Butt & Volkoff, 2019). For example, germ-free zebrafish treated with the bacterium *Lactobacillus plantarum* are able to attenuate stress-related behaviours (Davis *et al.*, 2016), and decrease the stress response by lowering the expression of corticotrophin-releasing hormone (CRH) (Forsatkar *et al.*, 2017). As discussed above, the stress response is a key factor that affects the feeding responses of fishes (Bonga, 1997). Therefore, interindividual differences in the gut microbiome of fish may interact with the stress response and other phenotypic traits to alter feeding, appetite and ultimately growth. Understanding which environments, microbes and/or diets promote a beneficial microbiome will be important to future studies assessing interindividual differences in fish growth.

7. Conclusions and future directions

The phenotype that promotes or drives better growth in some fish will be a consequence of complex interactions between a large number of genetic and non-genetic factors. The development of a beneficial growth phenotype depends on the interplay of the organism's own genetic make-up, the environmental experience of its parents and the environmental/social experiences during its own development (Fig. 2). External influences on phenotypic development are likely mediated in part by endocrine systems and resultant physiological processes. Based on the current gaps in knowledge, we suggest a number of research questions which will drive understanding of interindividual differences in fish growth:

1. How do parental influences impact offspring growth phenotypes?
2. What are the relative contributions of genetic vs. non-genetic influences on interindividual growth differences?
3. What are the relationships between organ size, digestive efficiency and growth?
4. What are the interindividual relationships between SMR, MMR, aerobic scope, PRAS, SDA, feed intake and growth?
5. How do interindividual differences in the SDA coefficient translate to differences in growth?
6. Are interindividual differences in predictive traits for growth maintained through time?
7. How does the gut microbiome interact with metabolism, behaviour and growth of individuals?
8. How are interindividual growth differences modulated by environmental parameters, and can we select genotypes/phenotypes with optimal performance in future environments?
9. Can gene knock-out experiments help to answer the above questions, and which target genes might prove most fruitful (e.g., digestive processes, protein synthesis)?

While the influence of genetic traits has played a role in the selection of fast-growing fish in aquaculture, there has been relatively little research attention given to other, non-genetic factors that play a role in determining interindividual growth phenotypes. We hope that this paper sparks further interest in this topic and paves the way for new insights into the question of why some fish grow faster than others.

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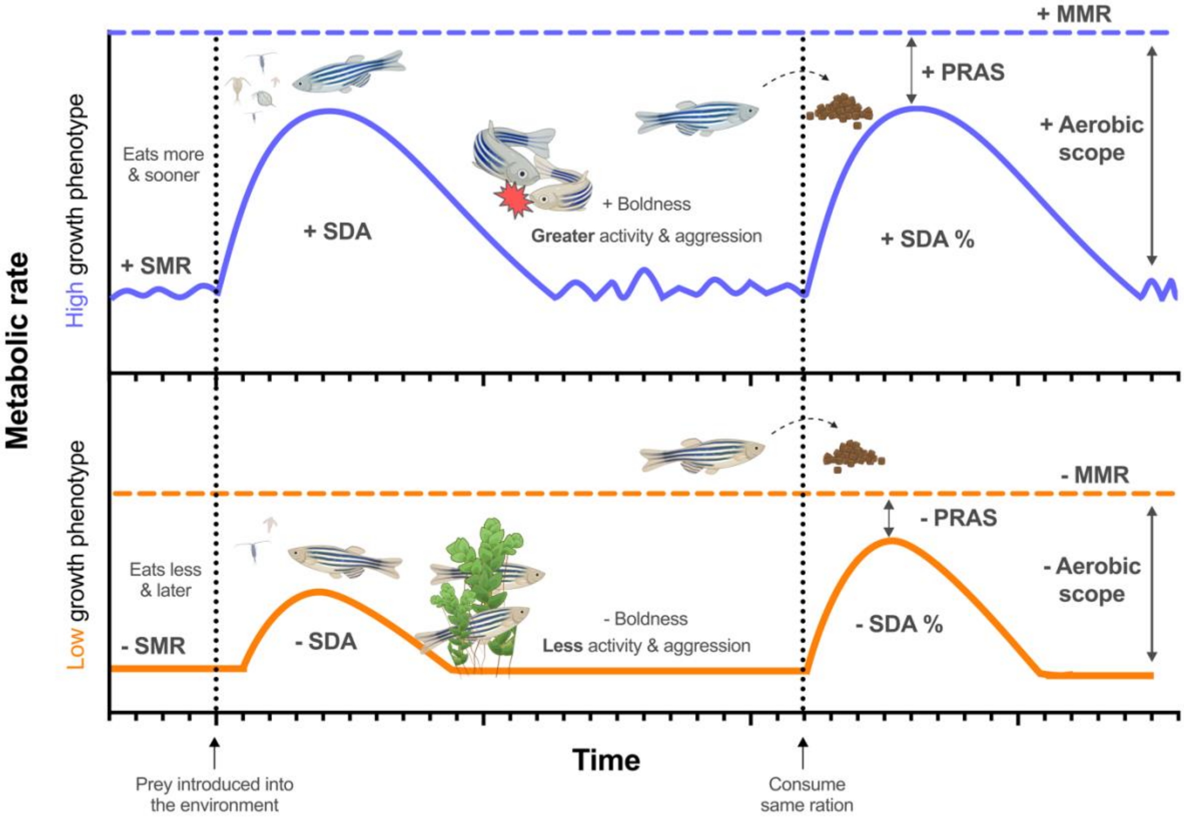

Figure 1: Conceptual diagram showing some of the traits of fish that may characterise a high-growth phenotype (blue) compared with a slow-growth phenotype (orange). Time could be equivalent to ~5 days. Symbols + and – indicate higher and lower levels, respectively. High-growth individuals may have a higher standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope. They may exhibit elevated boldness/aggression/activity and thus have higher metabolic requirements. When encountering prey in a competitive environment, high-growth individuals may consume lots of food quickly (resulting in a high specific dynamic action [SDA]), while slow-growth individuals may be submissive/hesitant and ultimately consume less food (lower SDA). When both high- and low-growth phenotypes consume the same sized ration, high-growth individuals may exhibit a greater SDA coefficient (SDA %) due to greater protein synthesis and anabolism. Despite the greater SDA coefficient, high-growth individuals may maintain a higher postprandial residual aerobic scope (PRAS) because of their elevated MMR.

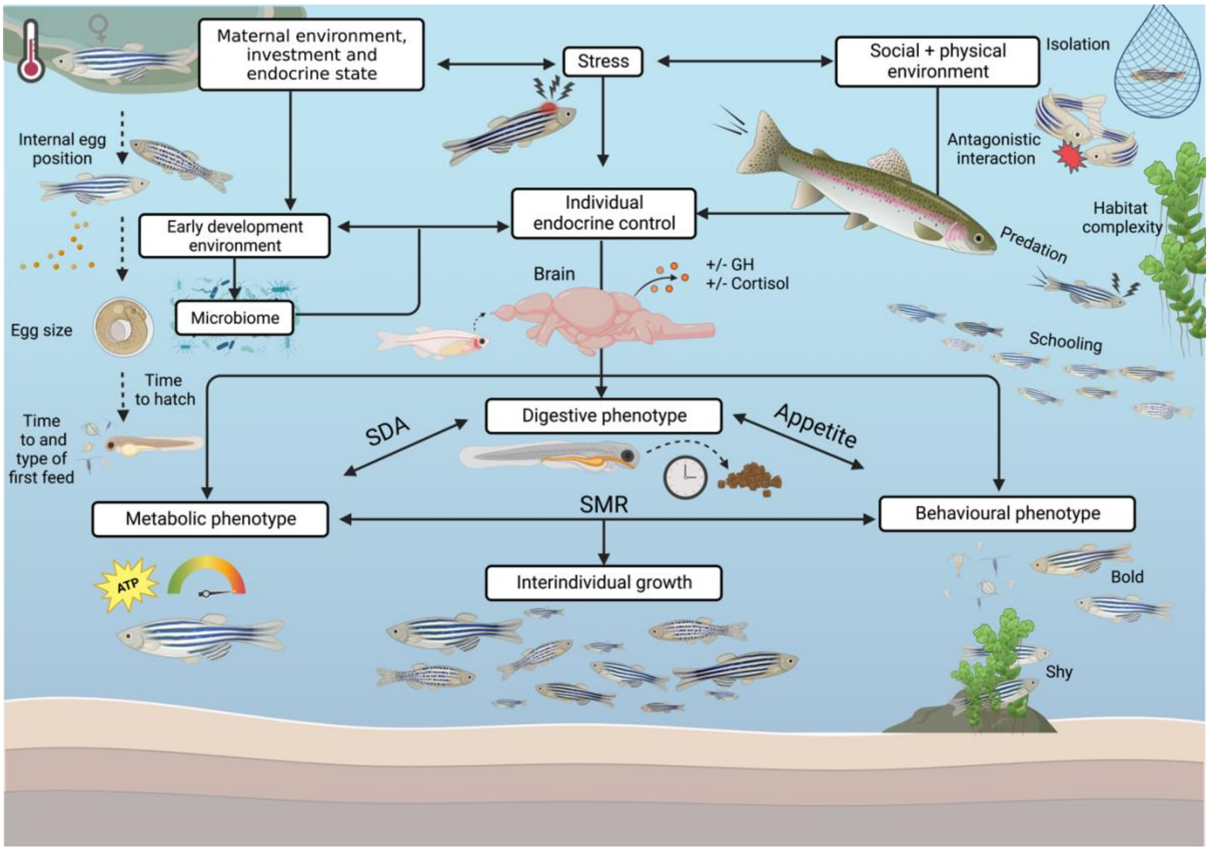

Figure 2: Schematic showing interactions between drivers of interindividual differences in fish growth. Individual variation in factors like stress, maternal investment/endocrine state, social interactions, and early development characteristics like time to hatch and/or first feed will all act on the fish brain and endocrine system (e.g., release of growth hormone (GH) or cortisol) to drive the development of phenotypes with differential energy use (the metabolic phenotype; e.g., specific dynamic action (SDA), standard metabolic rate (SMR)), energy uptake (the digestive phenotype; e.g., organ size and efficiency) and behaviour (the behavioural phenotype; bold, shy, dominant, subordinate). The presence of multiple metabolic, digestive and/or behavioural phenotypes will drive the development of interindividual fish growth within a closely related population.

Table 1: Summary of studies that have either directly or indirectly assessed drivers of interindividual differences in fish growth. Where available, positive (+), negative (-) and non-significant (n.s.) relationships between the driver, growth trait measured and/or interindividual fish growth are shown. Fish relatedness was left blank when information on parents was unavailable.

Species	Relatedness	Growth trait measured	Driver	Relationship to growth	Relationship to interindividual variation	Reference
Barramundi (*Lates calcarifer*)		SGR	SMR	+	NA	(Norin *et al.*, 2016)
Atlantic salmon (*Salmo salar*)		fork length at 2, 7 and 13 weeks	dominance + otolith size	+	NA	(Metcalfe *et al.*, 1992)
Steel head trout (*Oncorhynchus mykiss*)		wet and dry mass increase	dominance + social rank	+	+	(Abbott & Dill, 1989)
Atlantic salmon (*Salmo salar*)		SGR	aggression + rSMR	n.s.	n.s.	(Cutts, Metcalfe & Taylor, 1998)
Rainbow trout (*Oncorhynchus mykiss*)	Full siblings	SGR and FCR	ovine growth hormone treatment (NIDDK-oGH-15)	+	NA	(Johnsson & Björnsson, 1994)
Brown trout (*Salmo trutta*)	Full siblings	SGR	AS + SMR + food level	+/- dependent on food level	+/- dependent on food level	(Auer *et al.*, 2015)
Grass carp (*Ctenopharyngodon idella*)		SGR	SDA	+	NA	(Carter & Brafield, 1992)

Atlantic salmon (*Salmo salar*)		wet mass (over time) + feed intake	growth hormone transgene + boldness	+	+	(Abrahams & Sutterlin, 1999)
Masu salmon (*Oncorhynchus masou*)	Some full siblings	mass at day 0 and day 30	RMR + dominance	+	NA	(Yamamoto, Ueda & Higashi, 1998)
European eel (*Anguilla anguilla*)	Some full siblings	SGR	rSMR	+	NA	(Boldsen, Norin & Malte, 2013)
Brown trout (*Salmo trutta*)	Full siblings and half siblings	SGR	rSMR	- (variable through time)	NA	(Norin & Malte, 2011)
Brown trout (*Salmo trutta*)	Full siblings and half siblings	mass over time	SMR	n.s.	NA	(Álvarez & Nicieza, 2005)
African cichlid (*Haplochromis burtoni*)	Full siblings and half siblings	change in standard length over 7 days	social rank	-	NA	(Hofmann *et al.*, 1999)
Atlantic salmon (*Salmo salar*)		change in fork length at 1730 dd and 2842 dd	maternal cortisol	+ (offspring)	NA	(Eriksen *et al.*, 2007)
Atlantic salmon (*Salmo salar*)		change in fork length at 510 dd and first feeding 810 dd	maternal cortisol	- (offspring)	NA	(Eriksen *et al.*, 2006)
Rainbow trout (*Oncorhynchus mykiss*)		growth rate (g/day)	maternal stress	n.s.	+ (but not analysed)	(Contreras-Sánchez *et al.*, 1998)
Arctic charr (*Salvelinus alpinus*)	Some full siblings	SGR	dominance + aggression + swimming speed	+/- dependent on swimming speed and rank	NA	(Christiansen & Jobling, 1990)

Common carp (*Cyprinus carpio*)	Full siblings	SGR	growth hormone transgene	+	NA	(Li et al., 2007)
Southern catfish (*Silurus meridionalis*)		SGR	SDA	n.s.	NA	(Fu *et al.*, 2008)
Atlantic cod (*Gadus morhua*)		daily change in mass over 84 days + condition factor	HSI + mitochondrial enzyme CS activity in intestine	NA	+	(Couture, Dutil & Guderley, 1998)
Brown trout (*Salmo trutta*)	Full siblings	change in absolute size	dominance/rank + metabolism + shelter use + food availability	+/- dependent on food availability, rank and habitat use	NA	(Hoogenboom *et al.*, 2013)
Atlantic salmon (*Salmo salar*)	Some full siblings	SGR	RMR + habitat + food distribution/predictability	+/- dependent on habitat complexity and rank	NA	(Reid *et al.*, 2012)
Brown trout (*Salmo trutta*)		SGR	habitat complexity	+ dominant; - subordinate	+	(Höjesjö *et al.*, 2004)
Rainbow trout (*Oncorhynchus mykiss*)		SGR and FCR	stocking density + flow speed + sustained aerobic scope	+/- dependent on stocking density and flow	NA	(McKenzie *et al.*, 2012)
Brook charr (*Salvelinus fontinalis*)		SGR and FCR	stocking density + dominance + stress	-	NA	(Vijayan & Leatherland, 1988)
Atlantic salmon (*Salmo salar*)		SGR	metabolism + aggression	n.s.	NA	(SeppÄnen *et al.*, 2009)

Rainbow trout (*Oncorhynchus mykiss*)		SGR	restricted feeding + dominance/social hierarchies	+/- dependent on food availability and rank	+	(Jobling & Koskela, 1996)
Common carp (*Cyprinus carpio*)		mass increase over 6 weeks	transgene + gut microbiota	+	NA	(Li et al., 2013)
Rainbow trout (*Salmo gairdneri*)		individual mass gain and feed intake	number of pyloric caeca	+	NA	(Bergot *et al.*, 1981)
Cichlid (*Simochromis pleurospilus*)		SGR (% day) and digestive efficiency	juvenile food availability + digestive organ mass	+	NA	(Kotrschal *et al.*, 2014)
Grass carp (*Ctenopharyngodon idella*)		SGR (% day)	higher protein retention + lower protein degradation	+	NA	(Carter *et al.*, 1993a)
Chanchita (*Cichlasoma dimerus*)		condition factor, SGR (% day) and body mass after two months	sex size dimorphism	+/- dependent on sex	NA	(Delgadin *et al.*, 2014)
Haddock (*Melanogrammus aeglefinus*)		SGR (% day)	rate of energy loss	+	+ (but not analysed)	(Lankin *et al.*, 2008)
Atlantic cod (*Gadus morhua*)		growth in mm per day and mg per day	rate of energy loss	+	+	(Peck, Buckley & Bengtson, 2004)
Atlantic cod (*Gadus morhua*)		dry mass, body mass, and standard length over ten weeks	maternal mass and condition	+	NA	(Clemmesen *et al.*, 2003)

Atlantic cod (*Gadus morhua*)	Some full and half siblings	SGR	egg size	+	NA	(Marteinsdottir & Steinarsson, 1998)
Nile tilapia (*Oreochromis niloticus*)		feed intake, FCR, fish mass	stocking density	-	NA	(Azaza *et al.*, 2013)
Hybrid sunfish (green sunfish (*Lepomis cyanellus*) X bluegill (*Lepomis macrochirus*))	Some full siblings	SGR, feed intake	initial size	+	NA	(Wang et al., 1998)
Arctic charr (*Salvelinus alpinus*)	Some full siblings	SGR	isolation	+	+	(Jobling & Reinsnes, 1986)
Atlantic salmon (*Salmo salar*)		fork length and mass over time	NA	NA	NA	(Thorpe, 1977)
Atlantic salmon (*Salmo salar*)	Full siblings	length and mass	upper and lower modal groups + appetite	+	+ (but not analysed)	(Metcalfe, Huntingford & Thorpe, 1988)
Greenback flounder (*Rhombosolea tapirina*)	Full siblings	SGR	dominance + appetite/feed intake	+	+	(Carter *et al.*, 1996)
Atlantic salmon (*Salmo salar*)		SGR	Diploidy	+	NA	(Carter *et al.*, 1994)
Arctic charr (*Salvelinus alpinus*)	Full siblings	mass and length	Maternal effects and genetic contribution of hybrid crosses	+	NA	(March, 1991)
Atlantic salmon (*Salmo salar*) X Brown Trout (*Salmo trutta*) hybrids	Some full siblings	growth rate	Hybrid	+	+	(Galbreath & Thorgaard, 1994)

Shanny (*Lipophrys pholis*)		condition factor, change in mass over 5 weeks and 5 - 10 weeks	sight + smell of conspecific	-	NA	(Wirtz, 1974)
Cichlid (*Tilapia zillii*)	Full siblings	mass increase over time	dominance + appetite + food acquisition	+	NA	(Koebele, 1985)
Pygmy sunfish (*Elassoma evergladei*)		body mass over time (up to 175 days)	stocking density /competition	-	+ ovary size and egg number	(Rubenstein, 1981)
Arctic charr (*Salvelinus alpinus*)		SGR, feed intake	competition	NA	-	(Jobling & Baardvik, 1994)
Arctic charr (*Salvelinus alpinus*)		SGR	variation in size of individuals within a group	+	NA	(Baardvik & Jobling, 1990)
Brown trout (*Salmo trutta*)		SGR and FCR	high mitochondrial efficiency of ATP in the liver	+	NA	(Salin *et al.*, 2019)
Rainbow trout (*Oncorhynchus mykiss*)		SGR	meal size + Ucrit + endurance	+ meal size and endurance; - Ucrit	NA	(Gregory & Wood, 1998)
Rainbow trout (*Oncorhynchus mykiss*)		growth rate (% day)	protein synthesis	+	NA	(Houlihan, McMillan & Laurent, 1986)
Rainbow trout (*Oncorhynchus mykiss*)		protein growth (% per day)	protein synthesis	+	NA	(McCarthy *et al.*, 1994)
Pike (*Esox lucius*)		SGR	individual radial distance moved	+	NA	(Nyqvist *et al.*, 2018)
Turbot (*Scopo maximus*)		SGR and feed intake	dominance + rank	+	NA	(Irwin, O’Halloran & FitzGerald, 2002)

Turbot (*Scopo maximus*)		SGR and feed intake	stocking densities and hierarchies	NA	+	(Irwin, O’Halloran & FitzGerald, 1999)
Greenback flounder (*Rhombosolea tapirina*)		SGR	stocking densities and hierarchies	NA	+	(Carter *et al.*, 1996)
Dover sole (*Solea solea*)	Some full and half siblings	SGR	stocking density	NA	+	(Schram *et al.*, 2006)
Atlantic salmon (*Salmo salar*)	Full siblings	SGR (standard length mm)	time to hatch + alevin length at 116 dpf	+ hatch date; - alevin length	+	(Gilbey *et al.*, 2009)
Bluehead wrasse (*Thalassoma bifasciatum*)		otolith growth	larval duration + size at age	+	NA	(Searcy & Sponaugle, 2000)
Brown trout (*Salmo trutta*)	Some full and half siblings	body mass	maternal dominance/rank + egg position within mass	+	+	(Burton *et al.*, 2013)
Dorada (*Brycon moorei*)	Full siblings	growth (mm per day)	isolation + boldness/aggression	+ boldness; +/- isolation	- isolation	(Baras & Lucas, 2010)
European sea bass (*Dicentrarchus labrax*)		SGR	feed intake + dominance hierarchy	+	+	(Campeas *et al.*, 2009)
Atlantic salmon (*Salmo salar*)	Full siblings	time to triple in mass	GH transgene	+	NA	(Tibbetts *et al.*, 2013)
Orange fin anemonefish (*Amphiprion chrysopterus*)	Full siblings	SGR	Parental flow environment	+	NA	(Cortese *et al.*, 2022)
Clown fish (*Amphiprion percula*)		growth in mm	dominance hierarchies/social rank	+/-	+/-	(Buston, 2003)

Yellow perch (*Perca flavescens*)	Some full and half siblings	SGR	estrogen (Estradiol-17β (E_2))	+ (mediated by initial size or maturational status)	NA	(Malison *et al.*, 1985)
Yellow perch (*Perca flavescens*)	Some full and half siblings	SGR	estrogen (Estradiol-17β (E_2))	+ (mediated by initial size or maturational status)	+ (e.g., sex related dimorphic growth)	(Malison *et al.*, 1988)
Threespined stickleback (*Gasterosteus aculeatus*)	Full and half-siblings	SGR	exposure to predator	+ as juvenile - as adults (magnitude of relationship mediated by sex)	NA	(Bell *et al.*, 2011)

Specific growth rate (SGR), routine metabolic rate (RMR), feed conversion ratio (FCR), specific dynamic action (SDA), residual standard metabolic rate (rSMR), standard metabolic rate (SMR), days post-fertilisation (dpf), degree days (dd), hepatosomatic index (HSI), growth hormone (GH), aerobic scope (AS), NA (not applicable).