UNIVERSITÉ DU QUÉBEC

EFFET DE LA VÉLOCITÉ DU COURANT SUR LA PLASTICITÉ MORPHOLOGIQUE DES PREMIERS STADES DE DÉVELOPPEMENT DE LA TRUITE ARC-EN-CIEL (*Oncorhynchus mykiss*)

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RÉSUMÉ

La plasticité développementale procure un excellent contexte dans lequel il est possible d'examiner les implications écologiques des variations abiotiques auxquelles les poissons sont exposés. La vélocité du courant est reconnue pour induire de la variation morphologique chez les salmonidés. Cependant, la signification fonctionnelle de ces changements à travers les premiers stades de vie demeure peu documentée. L'objectif premier de cette étude est de déterminer l'effet de la vélocité du courant sur la plasticité morphologique des premiers stades de développement de la truite arc-en-ciel (*Oncorhynchus mykiss*). Pour ce faire, de jeunes alevins ont été soumis à quatre régimes constants de vélocité de courant (0,4, 0,8, 1,6 et 3,2 cm/s) durant une période de 100 jours. Les approches morphométriques traditionnelle et géométrique ont été employées pour caractériser les changements morphologiques entre les traitements durant l'ontogénie. Ces derniers se concentrent principalement sur les changements externes dans (1) la forme du corps, (2) la forme des nageoires et (3) l'arrangement spatial des nageoires des poissons. La plasticité morphologique induite par la vélocité du courant a été détectée dans toutes les classes de taille explorées (15-20, 20-25, 25-30 et 30-35 mm). Pour les plus grands poissons, les changements morphologiques dans la forme et la position des nageoires concordent avec les adaptations nécessaires à une meilleure performance de nage sous des habitats divergents. Toutefois, les changements dans la forme du corps répondent de façon inverse aux prédictions fonctionnelles, suggérant une réponse maladaptative face à la vélocité du courant. Il est suggéré que la forme du corps est contrainte par la réponse adaptative du système musculaire. Ainsi, même sous une pression de sélection similaire, le caractère multidimensionnel de la réponse d'un poisson (i.e., changements dans la morphologie, la physiologie et le comportement au cours de l'ontogénie) peut mener à des compromis et à des interactions complexes entre ses différents systèmes développementaux.

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INTRODUCTION GÉNÉRALE

La plasticité développementale est définie par la capacité d'un génotype donné d'emprunter différentes trajectoires ontogénétiques en réponse à des stimuli environnementaux (Smith-Gill, 1983; West-Eberhard, 2005a). Divers rôles évolutifs sont attribués à ce processus, dont celui d'engendrer de nouveaux phénotypes dans une population (Waddington, 1942; West-Eberhard, 2005a). En effet, outre les mutations, l'apparition de tels phénotypes dans une population peut se faire par la recombinaison développementale, c'est-à-dire la réorganisation d'une trajectoire ontogénétique pré-existante en réponse à des stimuli environnementaux (West-Eberhard, 2005a). Si le phénotype nouveau procure un avantage sélectif aux organismes le possédant, il est probable que sa trajectoire développementale se *canalise* (i.e. perte de flexibilité développementale facilitant l'obtention de ce phénotype; Waddington, 1942) jusqu'à éventuellement devenir *génétiquement assimilé* (i.e., obtention du phénotype en l'absence du stimulus original; Waddington, 1953) dans la population. Ainsi, la plasticité développementale permet d'introduire dans une population de nouveaux phénotypes pouvant être soumis à la sélection naturelle et entraîner des changements évolutifs importants.

Dans plusieurs cas, les modifications dans l'ontogénie induits par l'environnement mènent à de la plasticité phénotypique. Cette dernière est définie par la capacité d'un génotype donné de produire plus d'une forme alternative d'état morphologique, physiologique ou comportementale en réponse aux conditions environnementales (West-Eberhard, 1989). Cette plasticité possède aussi d'importantes conséquences évolutives. D'abord, la plasticité phénotypique permet à une espèce d'accroître sa distribution spatiale et ainsi de l'exposer à de nouvelles pressions de sélection, pouvant ainsi favoriser les changements génétiques (Stearns, 1989). De plus, elle permet d'accroître les chances de survie des espèces en augmentant leur niveau de tolérance lors des périodes critiques (Via et al., 1995), tel que durant un goulot d'étranglement, c'est-à-dire une réduction massive de la taille de la population suite à un événement quelconque (i.e. migration, catastrophe naturelle, etc.).

En milieu naturel, les poissons nordiques, notamment les salmonidés, présentent un haut niveau de plasticité morphologique (Dynes et al., 1999). En effet, les poissons nordiques d'eau douce présentent une grande variabilité morphologique, mais un très faible niveau de diversité génétique (Bernatchez and Wilson, 1998). Cette variation morphologique confère un excellent contexte dans lequel il est possible d'examiner les implications écologiques des variations abiotiques durant le développement d'un organisme (Hall and Wake, 1999).

L'ontogénie et la morphologie d'un poisson peuvent être influencées par différents facteurs environnementaux, dont la température (Pavlov and Moksness, 1997), la quantité de nourriture (Marcil et al., 2006) et la vélocité du courant (Grünbaum et al., 2007). Parmi ceux-ci, la vélocité du courant demeure un des facteurs les plus susceptibles d'affecter la morphologie d'un poisson, puisqu'il agit sur tous les aspects de la vie d'un poisson, incluant la locomotion, l'alimentation, l'évitement des prédateurs et les interactions sociales.

Le fait que certains morphotypes se retrouvent en constante association avec certains types d'habitats (e.g., benthique et littoral) suggère que cette plasticité correspond à une stratégie adaptative des poissons en réponse aux variations de leur environnement. Néanmoins, les variations morphologiques obtenues sous différents régimes de vélocité de courant ne peuvent être considérées adaptatives que si la direction des changements est congruente avec les prédictions basées sur les théories hydrodynamiques. Ainsi, les traits morphologiques qui sont les plus susceptibles d'affecter les performances de nage (i.e., nage soutenue, départs rapides et manœuvres) sont ceux liés aux coûts énergétiques, c'est-à-dire associés à la production des forces de poussée et de traînée (Lighthill, 1970; Webb, 1982).

Théoriquement, les poissons élevés en courants rapides devraient modifier la forme de leur corps et de leurs nageoires afin d'optimiser les performances pour la nage soutenue (Lighthill, 1970; Webb, 1982). La performance de nage soutenue est morphologiquement maximisée, entre autre, par un corps inflexible et élancé, un pédoncule caudal court et étroit, une nageoire caudale haute et des nageoires dorsale, anale et pectorales plus courtes (Lighthill, 1970; Webb, 1982; 1984; Webb and Weihs, 1986; Weihs, 1989; Drucker and

Lauder, 2003; 2005). Ces modifications permettent de maximiser les forces de poussée tout en minimisant les forces de traînée (Webb, 1982; 1984).

Au contraire, les poissons élevés dans des courants lents devraient modifier leur morphologie afin d'optimiser les performances durant les départs rapides et les manœuvres (e.g., virages brusques, freinages, nage sur place; Lighthill, 1970; Webb, 1982). Bien qu'utilisés dans tous les régimes de courant, les départs rapides sont en général rencontrés plus fréquemment en faible vélocité de courant. En effet, les départs rapides sont directement impliqués lors des comportements agressifs, lesquels sont reconnus pour diminuer en fréquence avec l'augmentation de la vélocité du courant chez les salmonidés (Cole and Noakes, 1980; Adams et al., 1995). Une morphologie optimale pour les départs rapides et les manœuvres est caractérisée, entre autre, par un corps haut et étroit, un pédoncule caudal long et large et de longues nageoires dorsale, anale et pectorales (Webb, 1982; 1984; Weihs, 1989; Lauder and Drucker, 2004). En général, ces modifications permettent de maximiser les forces de poussée, sans tenir compte des forces de traînée (Webb, 1982; 1984).

Ces prédictions d'association entre la morphologie et les variations dans la vélocité du courant ont été observées empiriquement sur les stades juvéniles et adultes de salmonidés (Pakkasmaa and Piironen, 2000; Imre et al., 2002; Peres-Neto and Magnan, 2004; Keeley et al., 2007). Cependant, la direction et l'intensité des réponses des traits face aux variations du courant peuvent varier à travers les espèces et les études indépendantes. À titre d'exemple, Peres-Neto et Magnan (2004) ont trouvé chez l'omble de fontaine des nageoires pectorales plus petites avec l'augmentation de la vélocité du courant, tandis que Imre et al. (2002) n'ont dénoté aucune différence chez cette espèce. Pakkasmaa et Piironen (2000), quant à eux, ont trouvé une réponse inverse chez la truite brune. Les disparités observées suggèrent une forte réponse spécifique au taxon, pouvant refléter des adaptations à des conditions à plus fine échelle (i.e., microhabitats) ou des chemins évolutifs différents entre les espèces (Robinson and Parsons, 2002; Peres-Neto and Magnan, 2004). Néanmoins, les connaissances sur l'obtention de ces divergences morphologiques de même que la signification fonctionnelle de ces changements demeurent encore peu documentées.

À l'exception de la récente étude de Grünbaum et al. (2007), les travaux portant sur la plasticité morphologique induite par la vélocité du courant chez les salmonidés se sont concentrés sur les stades juvéniles et adultes. Néanmoins, les connaissances des variations morphologiques des premiers stades de vie sont fondamentales à la compréhension des changements dans les demandes écologiques de l'espèce. Ainsi, il est suggéré que les patrons larvaires de changements de forme et de croissance sont des facteurs importants optimisant la survie et par conséquent maintenus au cours de l'évolution (Fuiman, 1983; Webb and Weihs, 1986; Osse, 1990; Osse et al., 1997; Hale, 1999). Cette relation entre la morphologie et la fonction peut se traduire par des adaptations afin d'optimiser divers paramètres de locomotion. Malgré tout, la relation entre la forme du corps durant le développement et les fonctions locomotrices ont reçu peu d'attention à ce jour.

Objectifs

L'objectif principal de cette étude est de déterminer l'effet de la vélocité du courant sur la plasticité morphologique des premiers stades de développement de la truite arc-en-ciel (*Oncorhynchus mykiss*). Pour ce faire, de jeunes alevins ont été soumis à quatre régimes de vélocité de courant (i.e., 0,4, 0,8, 1,6 et 3,2 cm/s) en conditions expérimentales contrôlées. La caractérisation des variations morphologiques est effectuée à l'aide de deux approches morphométriques (traditionnelle et géométrique) et se concentre principalement sur les changements externes dans (1) la forme du corps, (2) la forme des nageoires et (3) l'arrangement spatial des nageoires des poissons. La signification fonctionnelle des changements morphologiques est établie en comparant les réponses morphologiques obtenues avec les attentes fonctionnelles spécifiques à la truite arc-en-ciel.

Le présent mémoire est rédigé sous forme d'un article scientifique en anglais qui a été soumis pour évaluation dans la revue *Journal of Morphology*.

CHAPITRE PREMIER

EFFECT OF WATER VELOCITY ON EARLY DEVELOPMENTAL PLASTICITY OF RAINBOW TROUT: SHAPE AND FUNCTION

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ABSTRACT

Developmental plasticity plays a major role in evolution and provides an excellent context for unravelling the ecological implication of variation in abiotic factors to which developing fish are subjected. Water velocity has been known to induce morphological variations in salmonids, but the functional significance of these changes throughout early ontogeny are poorly documented. In this study, newly hatched specimens of rainbow trout (*Oncorhynchus mykiss*) were reared in four constant water-velocity treatments (0.4, 0.8, 1.6 and 3.2 cm/s) for a period of 100 days. Traditional and geometric morphometrics were used complementarily to characterize morphological changes among treatments during ontogeny. Morphological plasticity induced by water velocity was detected in all size classes (15-20, 20-25, 25-30 and 30-35 mm). In the largest size class, induced morphological changes in fin shape and position were consistent with adaptations required for improved swimming ability under divergent swimming demands. However, body shape changes responded inversely to functional expectations, suggesting that body shape response to water velocity is maladaptive. This response might be caused by constraints imposed by the adaptive response of the muscular system to water velocity. Therefore, even under the same selective pressure, the multi-dimensionality of a fish response (i.e., changes in morphology, physiology and behaviour through ontogeny) can lead to complex interactions and compromises among its different developmental systems.

INTRODUCTION

Developmental plasticity or the ability of a single genotype to adopt different developmental paths in response to the different ecological factors of its habitat can play a major role in evolution (Smith-Gill, 1983; West-Eberhard, 2005a). This ontogenetic process is believed to be implicated in the origin of species differences and phenotypic novelties (Waddington, 1942; West-Eberhard, 2005a). Furthermore, phenotypic variations that arise as a result of developmental recombination may play important roles in population divergence and speciation in fish assemblages (Smith and Skúlason, 1996). Therefore, developmental plasticity provides an excellent context in which to examine the mechanisms responsible for plasticity and the ecological implications of variation in abiotic factors to which developing fish are subjected (Hall and Wake, 1999).

Water velocity is an abiotic factor ubiquitous in all fish locomotor activities including foraging and predator avoidance. It is known to have a direct impact on swimming kinematics (Webb, 1971; Webb et al., 1984), aggressive behaviour (Cole and Noakes, 1980) and muscle development (Greer-Walker and Emerson, 1978; Nahhas et al., 1982) of salmonids. Northern fishes are known to show high level of morphological plasticity (Bernatchez and Wilson, 1998), which is suggested to be an adaptive response to changes in their environment. Morphological plasticity induced by water velocity variation has been demonstrated experimentally in salmonids (Pakkasmaa and Piironen, 2000; Imre et al., 2002; Peres-Neto and Magnan, 2004; Grünbaum et al., 2007; Keeley et al., 2007). In these studies, several traits showed inconsistent plastic responses among species. For instance, pectoral fin length decreased with water velocity in *Salvelinus fontinalis* and *S. alpinus* (Peres-Neto and Magnan, 2004), whereas it increased in *Salmo trutta* (Pakkasmaa and Piironen, 2000). These differences among species may reflect taxon-specific responses or adaptations to finer level conditions (i.e., microhabitats) (Robinson and Parsons, 2002; Peres-Neto and Magnan, 2004). Yet, no further examinations have been carried out to reveal the specific functional significance of these morphological differences.

The morphological changes obtained under differential water velocity treatments are thought to be adaptive if the direction of the response among treatments is consistent with the functional expectations. Fish reared in fast velocity flow are predicted to modify their body shape and morphological structures in a way that maximizes swimming efficiency and minimizes drag production during steady swimming (Lighthill, 1970; Webb, 1982; 1984; Webb and Weihs, 1986; Weihs, 1989). In contrast, slow velocity fish are expected to modify their morphology in order to improve fast-start performances and slow velocity maneuvers (Webb, 1982; 1984; Weihs, 1989; Lauder and Drucker, 2004). Although fast-starts are used at all water velocities, they are expected to be used more frequently in slow velocity treatments because of their importance in fish interactions and aggressive behaviour, which are known to be more frequent in slower water velocities (Cole and Noakes, 1980; Adams et al., 1995).

The early development of fish is a highly dynamic process in which changes in shape are expected to reflect adaptation to the immediate environmental conditions (Fuiman, 1983; Webb and Weihs, 1986; Osse, 1990; Osse et al., 1997; Hale, 1999). Therefore, information on early developmental stages is fundamental to understand the changing ecological requirements of a species. Nevertheless, with the exception of the recent study by Grünbaum et al. (2007), studies on morphological plasticity induced by water velocity have mainly focused on juvenile and adult stages and the relation between shape and locomotor functions in early developmental stages has received limited attention in salmonids.

Therefore, the main objective of this study is to assess morphological plasticity induced by differential water velocity regimes in laboratory-reared rainbow trout (*Oncorhynchus mykiss*). Our study provides exhaustive shape description of developmental plasticity in body shape, fin shape and fin position in early developmental stages using both traditional and geometric morphometrics.

MATERIAL AND METHODS

Specimens and rearing conditions

Approximately 10 000 diploid female eggs of rainbow trout, *Oncorhynchus mykiss* (Walbaum), were obtained from Troutlodge Inc. (Sumner, Washington, USA) in June 2005. Eggs were bred from one male and four females in order to minimize genetic variation, which is expected to improve the power of tests to discover the environment-phenotype relationships in experimental design (van Noordwijk, 1989). Prior to the experiment, eggs were disinfected with Wescodyne (Aquamerik, Québec, Canada), equally separated into eight lots and directly incubated in rearing canals. The experimental set-up consisted of a recirculating water system (Aquabiotech Inc., Québec, Canada) made of eight swimming canals, each having independent water velocity (uniform laminar flow) and temperature control systems (for details see Grünbaum et al., 2007). In order to eliminate potential bias owing to canal effects, inversed canal order was used from the previous study on *Salvelinus alpinus* (Grünbaum et al., 2007). Incubation parameters (9.2±0.3°C; pH 7.6±0.2) were held constant. Cleaning maintenance and dead eggs removal were performed daily.

Four days after the very first hatching, over 85% of hatching was reached in all canals and remaining unhatched eggs were removed. This day was fixed as the 0 day post-hatching (dph) of the experiment. Alevins (~950 per canal) were exposed for a period of 100 days to four constant water velocity treatments with one replicate per velocity: A = 0.4 cm/s (still), B = 0.8 cm/s (slow), C = 1.6 cm/s (medium) and D = 3.2 cm/s (fast). Treatments will be referred to by their respective letters (A-D) thereafter.

Water temperature (12±1°C), photoperiod (12h:12h L:D) and light intensity (~75 lux) were held constant after a two week acclimation period. Temperature, pH, dissolved O_2 concentration, ammonia and nitrate were monitored daily and kept within the species tolerance limit (Molony, 2001). From 15 dph, corresponding to a 75% yolk-sac absorption, to 26 dph, a diet based on Artemia (Aquamerik, Québec, Canada) enriched with Selco (Brine Shrimp Direct, UT, USA) was used to stimulate active feeding of alevins.

Thereafter, fish were fed to satiation twice a day with adapted trout pellets (Nutra HP, Skretting, New Brunswick, Canada). In all canals, mortality rate was lower than what was found in previous exercise experiments of salmonids (Greer-Walker and Emerson, 1978; Totland et al., 1987). However, total mortality was slightly higher in one canal of treatment A compared to other canals (11% vs 6% in all other canals; ANOVA : df = 7; F = 3.599; *P* = 0.001). We could not identify a specific cause for the higher mortality in this canal. Four specimens per canal per day were randomly captured with a dip net for the entire rearing period of 100 dph. Samples were fixed in neutral buffered formalin for 48 h, and then preserved in 70% ethanol.

Data acquisition

Specimens sampled from even days were processed for quantitative analyses of external morphology. For specimens below 33 mm standard length (SL), digital images of the left-lateral and ventral views of fish were captured using a Qicam digital camera with CCD sensor (Meyer Instruments, TX, USA) mounted on a Leica MZ16A binocular microscope, whereas images of larger specimens were taken with an Olympus Camedia C5060 digital camera. A rectangular plastic box with horizontal and vertical transparent strings was used in order to maintain a similar body orientation and fin positioning among specimens.

The analyses of morphological ontogenetic changes are based on both landmark coordinates and interlandmark distances (ILD) analyses. For geometric analyses, 12 lateral

(Fig. 1A) and eight ventral landmarks (Fig. 1B) were digitized on each image using tpsDIG32 (Rohlf, 2005a). Landmarks were chosen based on structure homology and optimal coverage of the morphology (Zelditch et al., 2004). For traditional analyses, 12 lateral (Fig. 1C) and four ventral ILD (Fig. 1D) were calculated using coordinates obtained from the set of landmarks used in geometric analyses and from additional landmarks. Linear distance measurements were modified from Peres-Neto and Magnan (2004) and selected in order to reflect characteristics that are hypothesized to be of primary importance for fish locomotion (Webb, 1982; 1984; Weihs, 1989; Lauder and Drucker, 2004; Drucker and Lauder, 2005).

Developmental plasticity of body shape and fin position using geometric morphometrics

Geometric morphometrics express and retain information about the spatial variation among landmark variables (Bookstein, 1991). Thus, relative to traditional morphometrics, the use of geometric methods for detecting body shape differences presents many advantages, including higher statistical power and a better comprehensive graphical representation of shape differences (Rohlf and Marcus, 1993; Rohlf, 2000; 2003a).

Each analysis begins with a generalized Procrustes analysis (GPA) (Dryden and Mardia, 1998) which superimposes configurations in order to eliminate the non-shape variation in terms of position, scale and orientation. First, centroids of each configuration are aligned on a common origin. Each specimen is then scaled to unit its centroid size (CS), a measure of size independent of shape in the absence of allometry (Bookstein, 1991). Next, specimens are rotated optimally to minimize the Procrustes distance (square root of the sum of squared differences between corresponding landmarks), a measure also used to quantify the amount of difference between any two shapes (Bookstein, 1991). Configurations are projected to a linear space (Kendall tangent space) appropriate for multivariate analyses (Slice, 2001). Mean configuration of landmarks was always used as the reference form to insure minimal distortions between shape space and the projected tangent space, which was confirmed ($r^2 = 0.99971-0.99981$, $P < 0.001$) using tpsSmall (Rohlf, 2003b).

Data treatment

Geometric analyses require complete and comparable sets of landmarks among specimens (Adams et al., 2004). Fin insertion landmarks were often missing for the first few days of development because fin structures were not completely formed or obliterated by finfold. Therefore, specimens younger than 20 dph had to be dismissed from the analyses. Images of damaged and deformed specimens or fish with their mouth wide open were excluded from the dataset. Statistical outliers were identified and removed from the dataset in a preliminary analysis using a principal component analysis (PCA) on the pooled samples. There were no significant differences in mean shape between replicates within each treatment (Goodall's F-test; all $P > 0.05$). Therefore, the data for a given treatment were pooled. A total of 1289 lateral and 1278 ventral images were kept for the analyses.

Body bending removal

Body bending occurred during preservation of specimens in ethanol and was not owed to any malformations. A PCA confirmed that body bending represented the main source of variation on the first axis for both lateral (PC1: 42.75%) and ventral (PC1: 70.60%) views. To correct for body bending, shape coordinates were regressed on loadings of the first principal component and standardized on a common value corresponding to a straight fish using Standard6 software (Sheets, 2001).

Developmental classes

To examine morphological plasticity throughout early development, shape ontogeny needed to be partitioned into meaningful developmental classes. Hence, knowledge of the most suitable proxy for ontogeny in relation to morphological development is necessary (Zelditch et al., 2000). Because both age (dph) and size (standard length [SL] and centroid size [CS]) were available, the selection of a proxy was addressed by regressing shape coordinates of unbent fish in each treatment from lateral and ventral views against all three proxies. Procrustes distance between each specimen and its expected shape was used to calculate the variance in the shape data that was unexplained by variation in the proxies (Zelditch et al., 2004). The lowest unexplained variance was used to determine the best statistical proxy for early morphological ontogeny. Regressions and unexplained variance computations were performed using tpsRegr (Rohlf, 2005b). In all cases, CS showed the lowest unexplained variance, followed by SL and then age (Table 1). Although CS is statistically the best proxy, its use has a limited application in comparative morphological studies because it varies with both the number and the choice of landmarks considered, which are rarely similar among studies. Furthermore, because CS values cannot be obtained without computation, its absolute values are not intuitively instructive without complementary information. For these reasons, SL was chosen over CS as the proxy for morphological ontogeny. The ontogeny of shape was separated in four size classes (i.e., 15-20, 20-25, 25-30 and 30-35 mm SL) in order to have comparable and large enough sample sizes (Table 2).

Assessment of allometry

Allometry has important consequences for shape variation analyses of fishes (Loy et al., 1998; Reis et al., 1998). To detect and correct for allometry, shape coordinates of specimens were regressed on CS for 32 samples defined by treatments (A, B, C, D), fish views (lateral and ventral) and size classes (15-20, 20-25, 25-30, 30-35 mm). Significance of allometric relations was tested using a Goodall's F-test (Goodall, 1991) within each sample. All except one sample showed significant allometry (Table 3). Allometry was corrected by regressing shape coordinates on corresponding CS and by standardizing on a similar mean CS for each sample using Standard6 (Sheets, 2001).

Statistical analyses

To assess shape differences among treatments within each size class, canonical variates analysis (CVA) was performed on partial warps and uniform component scores extracted from GPA. Canonical variates analysis creates axes (canonical variates, CVs) that maximize among-group variability relative to within-group variability (Albrecht, 1980). Wilks' Lambda was used to assess for general differences in shape among treatments in each size class (Dryden and Mardia, 1998). The number of meaningful axes was determined by a Bartlett's test (for details see Zelditch et al., 2004). In order to determine treatment wise differences, pairwise comparisons of Procrustes distances between each treatment's mean shape were performed on lateral and ventral views using TwoGroup (Sheets, 2000). Statistical significance was determined with a Goodall's F-test (Goodall, 1991; Rohlf, 2000). A Holm's sequential Bonferonni correction (Holm, 1979) was applied to reduce the probability of spurious results from multiple comparisons.

To interpret shape differences among treatments, thin-plate spline (Bookstein, 1991; Dryden and Mardia, 1998) deformation grids were used to depict differences of significant CVs using CVAGen6 (Sheets, 2002). Thin-plate spline is a deformation technique that uses minimal bending energy functions to map the relative location of points in the initial configuration to their corresponding location in the target form exactly.

Developmental plasticity of body and fin shape using traditional morphometric

Geometric analysis of landmark data requires strict and specific assumptions that preclude fin shape analyses. Because fins could not be oriented in the exact same position for all specimens during the image capture, fins occupied a multitude of angles and orientations that were reflected in the geometric analyses. This non-shape variation was shared among several multivariate axes, making it hard to correct for without undesirable effects on other shape variables. Therefore, the use of less restrictive, but less powerful methods of traditional multivariate analyses of linear distances was necessary.

Size correction

The difficulty of choosing among many competing methods for size-adjustment in traditional methods (Reist, 1985; Adams and Rohlf, 2000) is eluded in landmark based studies by the use of CS as a proxy of size (Bookstein, 1991). To separate size from shape variation, ILDs of each specimen were scaled to unit their corresponding lateral or ventral CS. However, the CS values used were not based on the actual set of landmarks applied to extract the ILD of body and fin morphology, because fin related landmarks can induce bias in the estimation of CS (i.e., fins adducted on the body will contribute to diminish real CS values, whereas fully extended fins will overestimate CS). Therefore, CS values previously obtained from the geometric morphometric analyses of lateral and ventral body shape were used for size correction.

Statistical analyses

Normality for 13 of the 16 traits was confirmed with a Lilliefors test. Because non-normality in multivariate analyses has limited affects when using reasonably large sample sizes (Reist, 1985), analyses were carried out on the raw size-adjusted linear distances. Discriminant Function Analysis (DFA) was used to assess for morphological differences in overall morphology among the four treatments for each size class. Statistical analyses and graphical depictions of linear distances data were performed using Systat Version 11 (SPSS Inc., Chicago, IL).

RESULTS

Shape differences among treatments using geometric analyses

Plots of the first two CVs of each size class are presented with associated deformation grids depicting morphological differentiation along significant axes for both views (Figs. 2-5). For all size classes, the four treatments overlap greatly with respect to both axes.

15-20 mm size class (~20-40 dph)

The 15-20 mm class show significant differences in morphological shape among the four treatments for both lateral (Wilks' Lambda = 0.591, $P < 0.0001$) and ventral (Wilks' Lambda = 0.731, $P < 0.0001$) views, indicative of an early shape response.

For the lateral view (Fig. 2A), CV1 sets the two faster velocity treatments apart from the two slower treatments. Specimens reared in faster treatments are characterized by a more anteriorly positioned dorsal fin and a slender body indicated by an inner insertion of the pelvic fins. The second axis separates treatment A from the other treatments. Specimens from treatment A are characterized by a higher pectoral fin insertion. Procrustes distances comparisons show that the two faster treatments are the only two groups not significantly different from one another in their overall shape, indicating a clear segregation between the faster and the slower treatments (Table 4).

For the ventral view, the only significant CV segregates groups following a A-B-D-C shape gradient (Fig. 2B). Traits that discriminate best among treatments are the mid-body width and the caudal peduncle, which are respectively narrower and longer for the faster velocity specimens. Procrustes distances comparisons indicate that treatment A is significantly different in overall shape from treatments C and D, whereas treatment B is only significantly different from treatment C (Table 4).

20-25 mm size class (~40-60 dph)

The four treatments in the 20-25 mm class differ significantly in their average body shape for lateral (Wilks' Lambda = 0.638, $P < 0.0001$) and ventral (Wilks' Lambda = 0.771, $P < 0.0001$) views.

For the lateral view (Fig. 3A), CV1 discriminates the two faster treatments from the two slower treatments following a A-B-D-C shape gradient. Specimens from treatments C and D are characterized by a more anterior dorsal fin, a more posterior adipose fin and a longer anal fin base positioned lower on the body. Following a similar shape pattern than in the 15-20 mm class, the second axis separates treatment A from the other treatments. Specimens from treatment A are characterized by a higher and more posterior pectoral fin insertion. Based on Procrustes distances comparisons, the only significant difference in overall shape is found between treatments A and C (Table 4).

For the ventral view (Fig. 3B), CVA analysis indicates a similar shape response than the one previously found from the 15-20 mm class. The same shape gradient (A-B-D-C) is found and specimens from treatments C and D are also characterized by a narrower mid-body and longer caudal peduncle. Procrustes distances comparisons indicate that treatments A and B differ significantly from treatment C in their overall shape, whereas only treatment A differs significantly from treatment D (Table 4).

25-30 mm size class (~60-80 dph)

The 25-30 mm class shows significant differences in morphological shape among the four treatments for both lateral (Wilks' Lambda = 0.581, $P < 0.0001$) and ventral (Wilks' Lambda = 0.789, $P < 0.0001$) views.

For the lateral view, CV1 positions the four groups along a A-B-D-C shape gradient (Fig. 4A). Specimens from faster treatments are characterized by a longer dorsal fin base and a higher caudal region, particularly near the anal fin. The second axis separates treatment A from treatment B with faster treatments as intermediate values. Specimens from treatment A are distinguished from specimens from treatment B by more anterior pectoral fins and a slightly shorter caudal peduncle. All treatments are significantly different from one another in their overall shape (Table 4).

For the ventral view, the first CV separates groups following the usual A-B-D-C shape gradient (Fig. 4B). Specimens from faster treatments are characterized mainly by a longer caudal peduncle. Procrustes distances comparisons significantly separate treatment A from other treatments in term of overall shape (Table 4). Treatments C and D are also significantly different from one another in their overall shape.

30-35 mm size class (~80-100 dph)

The largest size class show significant differences in morphological shape among the four treatments for both lateral (Wilks' Lambda = 0.545, $P < 0.0001$) and ventral (Wilks' Lambda = 0.614, $P < 0.0001$) views.

For the lateral view, the first CV presents a slightly different shape gradient (B-A-D-C) from what is usually observed in other size classes. The first CV mostly separates the two slower treatments from the two faster treatments (Fig. 5A). Specimens from faster treatments are characterized by a shorter jaw, a longer dorsal fin base, a higher body, a more anterior anal fin and more posterior pelvic fins. On the second axis, treatment A and to a lesser extent treatment C are separated from treatments B and D. The distance separating the dorsal and adipose fins is shorter and the caudal peduncle is higher for specimens from treatments B and D. Procrustes distances comparisons indicate that treatments C and D are similar in their overall shape (Table 4). Procrustes distances are higher when comparing the two slower with the two faster treatments.

Contrary to any other ventral analyses, two axes are significant from the CVA (Fig. 5B). The first axis divides groups along the usual shape gradient (A-B-D-C). Specimens from faster treatments show a narrower mid-body region and a longer caudal peduncle than specimens from slower velocities. The second CV separates treatment D from the three other treatments. Individuals from treatment D are characterized by a wider head and mid-body and a longer caudal peduncle. Procrustes distances comparisons of lateral and ventral views indicate that similarity in overall shape are observed only between treatments C and D. Procrustes distances are again higher when comparing the two faster with the two slower treatments (Table 4).

Shape differences among treatments using traditional analyses

In all size classes, the DFAs indicate that the four treatments are distinct in multivariate morphological space (15-20 mm: Wilks' Lambda = 0.4761, $P < 0.0001$; 20-25 mm: Wilks' Lambda = 0.5598, $P < 0.0001$; 25-30 mm: Wilks' Lambda = 0.4910, $P < 0.0001$; 30-35 mm: Wilks' Lambda = 0.497, $P < 0.0001$). Figure 6 displays plots of the two dimensions that distinguish maximally among treatments for each size class. For all size classes, the first dimension always segregates treatments following a A-B-D-C shape gradient. Canonical discriminant functions standardized by within variances of the first two axes are presented in table 5. The first two axes always account for more than 85% of total dispersion.

For the smallest size class, traits discriminating the best among treatments on the first axis are CPW and BH and to a lesser extent PFL, SL, HH, HW and CFL. Specimens from faster velocity treatments are characterized by a longer and slender body, a deeper but narrower head, a wider caudal peduncle, a shorter caudal fin and longer pectoral fins. For the second axis, MBW and DFB are the most discriminating traits, followed by CFH and DFL. Specimens from treatment B and to a lesser extent from treatment D are defined by a wider body, a shorter dorsal fin base, but a longer dorsal fin and a smaller caudal fin height compared to individuals reared in treatments A and C.

For the 20-25 mm class, the first axis indicates that specimens from faster treatments are characterized by a slender body, a deeper and narrower head, a deeper and wider caudal peduncle, a smaller caudal fin height and shorter pelvic fins. The second dimension separates treatment D from the three other treatments. Fish from treatment D were defined by a narrower body, a higher head, a shorter dorsal fin and longer anal and pectoral fins.

For the 25-30 mm class, the first axis shows that specimens from faster velocities are characterized by a slender body, a longer and narrower head, a deeper and wider caudal peduncle, a longer dorsal fin base and a shorter anal fin. The second axis separates again treatment D from the three other treatments. Fish from treatment D are defined by wider body and head, a narrower caudal peduncle, a shorter dorsal fin and a smaller caudal fin height.

For the largest size class, the first axis shows that fish from faster velocity treatments are characterized by a shorter body, a deeper and wider caudal peduncle and shorter dorsal, anal and pelvic fins. The second axis mostly isolates treatment B from the other treatments, but shows a very low dispersion value (8.8%). Specimens from treatment B are defined by a narrower body, a shorter but higher head and a shorter dorsal fin base.

Table 6 summarizes the main morphological traits determined by the two analytic methods that are associated with specimens reared in faster velocity treatments throughout their ontogeny.

DISCUSSION

This study is the first to provide an exhaustive shape description of early developmental plasticity induced by water velocity in *Oncorhynchus mykiss* using both traditional and geometric methods. It reveals three major points. (1) Water velocity induces morphological differences for the four size classes investigated. (2) In the 30-35 mm class, not all shape components respond conformingly to functional expectations, suggestive of a maladaptive body shape response. (3) Although most of the traits follow the same direction of response through ontogeny, some of the traits show complex non-directional responses across size classes.

Developmental plasticity assessment

Morphological plasticity induced by water velocity is confirmed in this study, as previously detected for alevin (Grünbaum et al., 2007), juvenile and adult salmonids (Pakkasmaa and Piironen, 2000; Imre et al., 2002; Peres-Neto and Magnan, 2004; Keeley et al., 2007). Shape differences among treatments is found in all size classes (i.e., 10-20, 20-

25, 25-30, 30-35 mm SL), indicating that morphological modelling is effective during the entire ontogeny and not restricted to any ontogenetic windows. Compared to the smaller size classes, larger size classes show an increase in Procrustes distances and in the number of significant differences in pairwise comparisons between treatments (Table 4), suggesting that morphological differences among treatments are accentuated with increase in size. However, our analyses cannot determine if this increase in disparity is caused by cumulative shape differences from previous size class, by increased shape differences produced within each size classes or both.

Differences in shape among treatments are small, but significant. This result was expected because phenotypic plasticity in *Oncorhynchus mykiss* has been known to account for only a small part (7.3%) of phenotypic variation found in natural habitats compared to heredity (52.7%) (Keeley et al., 2007). Nevertheless, small differences in morphology still might have important implications for swimming (for discussion see Webb, 1982; Imre et al., 2002).

Induced morphological plasticity of the 30-35 mm alevins

Our results reveal a clear dichotomy in mean shape between the two faster and the two slower water velocity treatments (Table 4). The overall and simplified morphological differences associated with faster velocity treatments are presented in table 6. These results arose from the use of two different morphometric methods (geometric and traditional). By doing so, we were able to extract complementary shape information hardly obtainable by using only one method. Geometric analyses provide clear information about fin position whereas traditional analyses capture information about fin shape. The fact that the two methods identified different structures as best discriminator among treatments is not surprising simply because different morphological traits are analysed. However, it should be noted that these differences never yielded contradictory directional responses. In order to reveal the functional significance of these morphological changes, comparisons are made using the largest size class (30-35 mm) as most of the hydromechanical predictions are based on juvenile or adult morphologies.

Body shape variation

A deep, short and laterally compressed body has been postulated to improve maneuverability and fast-start performances, whereas a long slender body is believed to favor sustained swimming (Webb, 1982; 1984; Taylor and McPhail, 1985; Walker, 1997). The optimum shape design of the caudal peduncle for sustained swimming performance is a slender and laterally compressed (also called narrow necking) morphology (Lighthill, 1970; Webb, 1982; 1984; Webb and Weihs, 1986). However, body shape analyses of the largest size class clearly contrast with these predictions. Relative to fish reared in slower velocities, fish from faster velocities have a more robust (short, deep and narrow) body and a caudal peduncle that is larger in all three planes. Therefore, our results suggest that body shape changes in *Oncorhynchus mykiss* induced by water velocity can be hydrodynamically maladaptive under particular experimental conditions.

Many studies on teleosts (e.g., Law and Blake, 1996; Schrank et al., 1999; Webb and Fairchild, 2001; McGuigan et al., 2003; Pon et al., 2007) have challenged the functional relationship between variation in body shape and higher swimming performance. Boily and Magnan (2002) demonstrated that in brook charr, stout fish had higher absolute swimming cost than slender fish. However, the higher net swimming cost was not related to body shape but rather to an indirect consequence of an increase in standard metabolic rate. Therefore, improved swimming performance can be achieved through different mechanisms or systems other than body shape variation alone.

An alternative hypothesis explaining this incongruity between induced morphological changes and functional expectations is that the body shape obtained is not an adaptation to reduce drag or increase swimming efficiency *per se*, but a byproduct of another internal adaptive plastic system, that is the increase in volume of propulsive musculature necessary for swimming. Thus, the likely maladaptive response of body shape to water velocity obtained in our study might be caused by the differential growth of muscle types under divergent swimming demands. In *Oncorhynchus mykiss*, red muscle is confined to a superficial layer near the lateral line and white (mosaic) muscle mostly makes up the trunk musculature (Johnston, 1975; Stickland, 1983; Rescan et al., 2001). The relative amount of red muscle generally increases towards the caudal peduncle in teleost fishes (Mosse and Hudson, 1977; van Raamsdonk et al., 1982; Totland et al., 1987). Slow steady swimming in *O. mykiss* is powered mainly by red muscle (Greer-Walker and Emerson, 1978; Nahhas et al., 1982), whereas higher power propulsions (fast-start and steady swimming > 3 body lengths/s [bl/s]) are mostly powered by white muscle (Hudson, 1973). Thus, continuously active fish (i.e., steady swimming speeds below white muscle recruitment) should have proportionately more red muscle, whereas fish that use more frequently fast-starts, such as in slow water velocity habitats, should have a greater proportion of white muscle (Mosse and Hudson, 1977; Webb, 1978; McLaughlin and Kramer, 1991). Therefore, the high, wide and long caudal peduncle of fast velocity fish might be a consequence of an increase in red muscle necessary for sustained swimming, whereas the wider mid-body (and perhaps consequently the smaller height) in slower velocity fish might be caused by an increase in white muscle.

Direct and indirect evidences exist for a relationship between higher red muscle proportion and greater sustained swimming ability in teleost fishes (Mosse and Hudson, 1977; McLaughlin and Kramer, 1991; McGuigan et al., 2003). However, studies specific to *Oncorhynchus mykiss* provide equivocal support to this hypothesis. Davie et al. (1986) revealed an increase in the proportion of red muscle relative to white muscle for trained fish (1 bl/s), but reversed trends or no effect were found in other studies (Greer-Walker and Emerson, 1978; Nahhas et al., 1982). Data on the effects of water velocity on the muscular system and on any other internal systems that might affect external body shape (e.g., skeletal system) of earlier developmental stages in *O. mykiss* are necessary to validate this hypothesis.

Fin shape variation

Rainbow trout's swimming gaits are known to vary with water velocity (Webb, 1971; Webb et al., 1984; Drucker and Lauder, 2003; 2005). At high steady swimming speed (over 2.0 bl/s), rainbow trout strictly adopt a body and caudal fin propulsion (BCF). At intermediate speed (0.5-2.0 bl/s), they use a combination of anterior median fin and body and caudal fin propulsion (M-BCF). At low speed (0-0.5 bl/s), they use a median and paired fin propulsion (MPF). Median and paired fins are usually more recruited during slow speed activities than during steady swimming at fast velocity. In general, longer fins are expected to enhance maneuverability and to maximize thrust production during fast-starts (Webb, 1984), whereas reduction of fin surface area may be an adaptation for drag reduction at higher swimming speed (Drucker and Lauder, 2003; Standen and Lauder, 2005). Therefore, fins are expected to be longer in fish reared in slow velocity environments. Our results from the 30-35 mm size class support this view as the dorsal, anal, pelvic and caudal fins are longer with decreasing water velocity. Only the pectoral fins show no plastic response. Comparisons with individual fin hydrodynamics of rainbow trout also suggest that these responses are adaptive to their specific environment.

In rainbow trout, the dorsal fin is actively recruited in several swimming activities including steady swimming, hovering, turning and braking (Drucker and Lauder, 2003; 2005). However, during steady swimming, involvement of the dorsal fin decreases with increasing swimming speed and the dorsal fin is no longer recruited at 2.0 bl/s (Drucker and Lauder, 2005). This fin also exhibits larger fin excursions during slow speed maneuvers than during steady swimming (Drucker and Lauder, 2005). Therefore, as dorsal fin seems to be more actively recruited in slow than in fast velocity environments, this fin should respond adaptively to enhance slow velocity performances. Our results for the 30-35 mm size class support this view as specimens reared in slower velocity treatments have a longer dorsal fin than specimens from faster treatments. Dorsal fin base is also larger for faster velocity specimens, but the hydromechanical significance for a broad fin attachment is not known at this time (Standen and Lauder, 2007).

No data on the hydrodynamics of the anal fin are available at this point for rainbow trout. Although anal fin has been found to possess a non negligible independent locomotor function from the dorsal fin in brook charr (Standen and Lauder, 2007), the fact that the anal fin exhibits in-phase excursion movements with the dorsal fin in rainbow trout (Drucker and Lauder, 2005) suggests that both dorsal and anal fins might share comparable locomotor functions. Our results support this view as anal fin is also longer in slow velocity specimens.

Pectoral fins of rainbow trout are completely inactive during fast steady swimming in microturbulent flow (Drucker and Lauder, 2003). Their recruitment is restricted to slow velocity activities such as hovering, turning and braking (Webb, 1971; Drucker and Lauder, 2003). Therefore, longer pectoral fins are expected in slow velocity treatments. However, our experiment indicates no noticeable difference in pectoral fin length among treatments. It has been suggested that pectoral fin length is genetically inherited rather than phenotypically plastic in the brook charr system (Proulx and Magnan, 2004). This could also be the case for *Oncorhynchus mykiss*.

No experimental hydrodynamic analysis of pelvic fins has yet been conducted. However, pelvic fins are known to play an active role during turning and braking maneuvers in rainbow trout (Drucker and Lauder, 2003; 2005). Our experiment shows longer pelvic fins in slow velocity fish, supporting the idea of an important role played by these fins during maneuvering in slow habitats. Quantitative hydrodynamic analyses of pelvic fins functions are needed to confirm this idea.

To date, fin forces during locomotion have not been measured for the caudal fin in rainbow trout. A high aspect ratio caudal fin has been hypothesized to be valuable for periodic propulsion in fishes, whereas a large surface area is considered favourable for high thrust production during fast-starts (Lighthill, 1970; Webb, 1982; 1984). Webb (1977) showed that caudal fin amputation was more detrimental for fast-start than cruising performances in rainbow trout suggesting that the principal function of caudal fin is found in fast acceleration rather than in steady swimming. Our results give support to this view as slow velocity fish have a slightly larger and higher caudal fin.

Fin position variation

Thrust can be enhanced through wake interactions between the dorsal/anal and the caudal fins (Lighthill, 1970; Drucker and Lauder, 2001; 2005; Standen and Lauder, 2005;

2007). Therefore, a rearward migration of the dorsal and anal fins is believed to be an adaptation for improved fast-start performances (Webb, 1982; Weihs, 1989). However, constructive hydrodynamic interactions may be less prevalent if the gap between dorsal/anal and caudal fins are relatively large (Drucker and Lauder, 2001; 2005). In rainbow trout, the dorsal fin is located more anteriorly on the body compared to the anal fin, which suggests that the anal fin may have a more important role than the dorsal fin for producing wakes that can be utilized by the caudal fin to enhance thrust during fast-starts (Drucker and Lauder, 2001; Standen and Lauder, 2007). Our results support this hypothesis as a posterior shift in anal fin is observed in slow velocity specimens from the 30-35 mm class, whereas dorsal fin only shows a negligible anterior displacement in faster velocity specimens (Fig. 5).

The function of the adipose fin for locomotion remains poorly understood. Drucker and Lauder (2005) demonstrated that in rainbow trout, this fin generated negligible motion independent of the body during steady swimming, but revealed a narrow drag wake, which might possess a role in locomotor force production. Reimchen and Temple (2004) detected significant effects of adipose fin removal on swimming kinematics for 7-12 cm rainbow trout, but not for smaller or larger specimens. In our study, the adipose fin shows a negligible anterior displacement in fast velocity specimens (Fig. 5), suggesting either a limited role of this fin position for locomotion or a weak level of plasticity.

An anterior positioning of pelvic fins has been proposed to be an adaptation for enhanced maneuverability in fishes (Webb and Weihs, 1986). Our results indicate that slow velocity fish have pelvic fins positioned more anteriorly (Fig. 5). However, studies on the hydrodynamics of the pelvic fins in rainbow trout are necessary to clearly interpret the functional significance of this change in position.

Therefore, induced morphological changes in the 30-35 mm class suggest that body shape maladaptive response to water velocity is the outcome of an adaptive plastic response of the muscular system. In other words, higher swimming performances are likely achieved by an increase in specific (red or white) muscle mass rather than by an optimization scheme for reduced drag and improved thrust of the body shape. However, assuming this hypothesis true, there is still no reason to suppose that the muscular system should restrain in any way the adaptive response of fin shape and position to water velocity. As expected, fin shape and position analyses of the 30-35 mm class seem free from this limitation as responses are generally congruent with functional expectations. Nevertheless, we prompt cautiousness in claiming the adaptiveness of obtained morphological changes as no fitness or swimming performances data were analysed in this study.

Ontogenetic changes in early development

Most of the morphological traits that segregate the faster and slower velocity treatments usually do so by following the same direction throughout ontogeny. For instance, a wider, longer and deeper caudal peduncle and a narrower body are observed in all size classes for faster velocity specimens. However, the direction and intensity of the response for some traits are not consistent throughout size classes. That is the case for body shape, which is slender and longer for high velocity fish early in the ontogeny, but switches to a deeper and shorter shape when reaching the 30-35 mm class. The adipose fin is positioned more posteriorly in faster velocity specimens for the two smaller size classes and switches to a negligible anterior position for the remaining of the ontogeny. The dorsal fin is positioned slightly more anteriorly in fast velocity specimens for the two smaller size classes, but no difference could be noticed for larger specimens. Pectoral fins are longer with increasing velocity in the smallest size class and identical among treatments for all other size classes. However, unravelling the functional significance of such complex morphological responses through ontogeny is extremely difficult as principles used to explain the functional morphology of adults is not applicable for younger stages. This is mainly owed to changes in hydrodynamic regimes and swimming modes during this period.

The hydrodynamic regime (viscous or inertial force dominated) in which fish must feed, breath and swim vary with both size and swimming speed (Lamb, 1932). The Reynolds number (*Re*) is the ratio of inertial to viscous forces and provides an indication of the nature of the hydrodynamic regime in which fish live in. The *Re* scales positively with both size and swimming speed (Lamb, 1932). Small size alevins usually swim in a viscous regime ($Re < 300$), virtually all adults swim in an inertial regime ($Re > 1000$) and both forces are to consider when *Re* is between these limits (McHenry and Lauder, 2005; 2006). Because the viscous regime is energetically more expensive than the inertial regime, morphological adaptations (e.g., elongated shape) are expected in order to prematurely exit the viscous dominated environment (Webb and Weihs, 1986; Fuiman and Webb, 1988; Fuiman and Batty, 1997). Rainbow trout alevins are also able to escape the viscous regime through behavioural adaptations such as fast-start performances (Gibb et al., 2006). However, at this point, we do not have sufficient information to assess the effects of variation in hydrodynamic regimes on the early morphological response of rainbow trout.

Whilst juvenile and adult rainbow trout can switch their swimming gaits depending on the variation in water velocity (e.g., BCF to M-BCF in slower velocities), smaller alevins can vary their swimming modes (defined by the degree of curvature of the body during steady swimming; Webb, 1971) with both ontogenetic stages and water velocity. Fish have been reported to use an anguilliform swimming mode early in the ontogeny and at low swimming speed and to progressively switch to a sub-carangiform swimming mode later in their development and in faster sustained swimming speeds (Osse, 1990; Osse and van den Boogaart, 1999; Müller and van Leeuwen, 2004). Sub-carangiform swimmers are assumed to be more efficient for steady swimming than anguilliform swimmers because a higher sustained swimming performance depends on a less flexible body (Webb, 1982; 1984). Therefore, fish reared in higher water velocities are expected to use more frequently the sub-carangiform swimming mode than slow velocity fish and morphological changes observed during early ontogeny might represent adaptations for higher performance in this mode of locomotion. Webb et al. (1984) examined variations in swimming kinematics during growth in rainbow trout, but not for specimens below 5.5 cm. Therefore, at this point, the functional significance of the morphological ontogenetic changes induced by water velocity treatments cannot be assessed without additional data on hydrodynamics and swimming kinematics of early developmental stages in rainbow trout.

Shape gradient versus water velocity gradient

Based on hydromechanical studies (Webb, 1982; 1984), as water velocity increases, a morphological gradient from a shape adapted to fast-starts and maneuvering to a shape adapted for steady swimming is expected. Therefore the morphological shape gradient should follow the same water velocity gradient. However, the first axis of all except two multivariate shape analyses (Figs. 3-6) indicates that the overall morphological gradient (A-B-D-C) do not match the predicted water velocity gradient (A-B-C-D). Fish reared in the fastest velocity treatment (D) show a morphology more comparable to fish from the slower treatments than do fish from treatment C. Although treatments C and D were only significantly different from one another in their overall shape for the 25-30 mm class (both lateral and ventral), the fact that the same shape gradient (A-B-D-C) is observed in a previous study using the same water velocity gradient (Grünbaum et al., 2007) remains intriguing. Assuming no rearing conditions or canal effects (see material and methods), why would an identical shape gradient emerges from both *Oncorhynchus mykiss* and *Salvelinus alpinus*? Two hypotheses are proposed to explain this similarity in shape gradient.

First, the physical stress caused by the fastest water velocity treatment (3.2 cm/s or ~2.7 bl/s for the smallest fish) might have over-passed the range of optimal conditions where adaptive phenotypes can be produced by the genotype (Newman, 1992). This situation could be represented by the right tail of a bell-shaped reaction norm (Stearns, 1989) in which extreme conditions are generally accompanied by a fitness or condition costs on the individual. However, no sign leads to the conclusion that treatment D represents a more stressful environment. The fastest water velocity (3.2 cm/s) used in this experiment is well below the limit of maximum sustainable swimming speed (*Ucrit*) (~5-7 bl/s) established for 8-10 cm rainbow trout (Hawkins and Quinn, 1996; Gregory and Wood, 1998). Also, such speed remains very low compared to velocities that can be encountered by fish in stream environments. The relative *Ucrit* usually increase with smaller size (Hawkins and Quinn, 1996). Although not measured in this study, agonistic behaviour is known to decrease with increasing water velocity in rainbow trout alevins (Cole and Noakes, 1980), suggesting lower energetic costs from aggressive activity in faster treatments (Adams et al., 1995). Mortality rate was not higher in the fastest treatment. Growth size (SL) was not affected by water velocity treatments (ANOVA : df = 3; F = 0.514; $P = 0.673$) in this study and was found to increase with faster velocities in Arctic charr (Grünbaum et al., 2007). Therefore, we are unable to find any evidence supporting this hypothesis.

An alternative hypothesis for this difference in shape gradient could rely on rainbow trout's behaviour in natural habitat. During early post-hatching ontogeny, rainbow trout larvae generally show a photonegative behaviour and remains buried in the substrate (Carey and Noakes, 1981). Up until near complete yolk-sac absorption (~20 dph; ~18.3 mm), larvae have no need to forage and acquire their energy through their yolk-sac. Although forcing fish to swim continuously already represents a novel environment, constraining larvae to swim in a high and sustained water velocity current (such as found in treatment D, but perhaps not in treatment C) during this specific endogenous feeding period might represent an ecological pressure never experienced and far more different than what can be found in natural habitats. This novel selective pressure, although apparently not lethal nor detrimental to larval growth (as mortality and SL are not different) is likely to affect the morphological adaptive responsiveness of the fish.

The direction to which environmental cues act into an individual's ontogeny depends, amongst other things, on the range of past environmental conditions experienced by its genotype (van Noordwijk, 1989; West-Eberhard, 1989). However, predicting the shape response of a fish faced to a novel apparently non-stressful environment remains largely exploratory. This situation could result in phenotypic accommodation in which adaptive plasticity is the likely response following the novel input during development (West-Eberhard, 2005b). In contrast, entering into a new environment that differs too greatly from the old one may produce plastic responses that are maladaptive (Price et al., 2003). Following this premise, we suggest that adopting a more generalist shape or a less specialized shape for sustained swimming (as observed in treatment D) could be beneficial (in term of survival) when coping with a never experienced environment, even if it implies the non-adaptation of fish with its actual environmental cues. This might explain the C and D reversal in the shape gradient, in which treatment C presents a more specialized shape for sustained swimming (at least for fin shape and position) than treatment D. Although this interpretation remains largely hypothetical, this situation represents a clear example of how reaction norm experiments can involve conditions never encountered in nature and how such situations can provide insights into evolutionary processes.

Our results suggest that contrary to fin shape and position, body shape responds maladaptively to water velocity for the 30-35 mm class. The adaptive response of the muscular system to water velocity likely constrains the body to adopt an inefficient hydrodynamic shape. Therefore, the same functional demand (e.g., higher or lower water velocity) can lead to complex interactions between the different developmental systems of a fish. The early ontogeny of fish being a highly dynamic process, it would be interesting to compare ontogenetic changes in the morphology with the swimming kinematics and the internal systems (i.e., skeletal and muscular) of rainbow trout during early development.

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Table 1. Percentage of unexplained variance obtained from shape coordinates regressions of each treatment on the three proxies (centroid size [CS], standard length [SL] and days post-hatching [dph]) for lateral and ventral views.

	Lateral			Ventral		
Treatments	CS	SL	dph	CS	SL	dph
A	92.30	92.80	94.20	59.90	61.10	69.10
B	94.80	95.30	97.30	61.20	62.40	71.60
C	91.40	92.00	93.80	64.30	66.10	72.70
D	93.70	94.20	95.80	68.60	69.80	76.30

Lower values indicate stronger allometric relations with the proxy. All regressions are significant ($P < 0.0001$). Note that in all cases, CS has the lowest unexplained value, followed by SL and finally dph.

Table 2. Sample sizes of the four treatments by type of analyses (geometric and traditional), views and size classes.

	Geometric								Traditional			
	Lateral				Ventral				Lateral and ventral			
	Size classes (mm) n = 1289				Size classes (mm) n = 1278				Size classes (mm) n = 1147			
Treatments	15-20	20-25	25-30	30-35	15-20	20-25	25-30	30-35	15-20	20-25	25-30	30-35
A	70	78	95	78	73	78	97	77	67	68	77	73
B	81	77	91	73	79	79	92	72	73	70	69	71
C	83	78	80	81	78	72	80	80	75	70	64	80
D	75	96	86	67	75	94	87	65	71	86	72	61
Total	309	329	352	299	305	323	356	294	286	294	282	285

Sample sizes of the three analyses (ventral and lateral geometric and traditional analyses) originate from the same initial set of specimens (n = 1629). Variation in sample size for the different analyses is owing to differential selection criteria for each method (see material and methods).

Table 3. Percentage of unexplained variance obtained from shape coordinates regressions of each group (treatment, size class and view) on their CS.

	Lateral Size classes (mm)				Ventral Size classes (mm)			
Treatments	15-20	20-25	25-30	30-35	15-20	20-25	25-30	30-35
A	95.32	97.65	95.36	91.84	96.84	90.56	94.16	85.16
B	97.41	**98.35**	97.97	94.40	96.44	93.97	92.03	76.11
C	96.96	94.16	96.72	93.36	95.95	92.62	88.22	74.32
D	95.15	97.21	97.34	92.20	97.37	91.15	96.33	78.24

Lower values indicate stronger allometric relations with CS. Significance of the relations was tested using a Goodall's F-statistic. The value in bold represents the only group without significant allometry ($P > 0.05$).

Table 4. Procruste distances of ventral (lower left) and lateral (upper right) views from pairwise comparisons between treatments.

	15-20 mm			
Treatments	A	B	C	D
A	-	**0.008**	**0.007**	**0.008**
B	0.005	-	**0.007**	**0.007**
C	**0.011**	**0.010**	-	0.005
D	**0.009**	0.007	0.004	-

	20-25 mm			
Treatments	A	B	C	D
A	-	0.005	**0.006**	0.005
B	0.005	-	0.006	0.005
C	**0.013**	**0.008**	-	0.004
D	**0.009**	0.005	0.004	-

	25-30 mm			
Treatments	A	B	C	D
A	-	**0.006**	**0.007**	**0.005**
B	**0.007**	-	**0.006**	**0.005**
C	**0.011**	0.005	-	**0.006**
D	**0.009**	0.004	**0.005**	-

	30-35 mm			
Treatments	A	B	C	D
A	-	**0.005**	**0.009**	**0.008**
B	**0.006**	-	**0.009**	**0.007**
C	**0.011**	**0.007**	-	0.004
D	**0.011**	**0.008**	0.005	-

Procrustes distances are calculated between consensus landmark configuration of each treatment. Values in bold indicate significant values after the Holm's sequential Bonferonni correction.

Table 5. The first two canonical functions standardized by within variances from the discriminant function analyses on size adjusted linear distance measures of each size class. See figure 1 for abbreviation of morphological traits.

Morphological trait	Size classes (mm)							
	15-20		20-25		25-30		30-35	
	1	2	1	2	1	2	1	2
SL	**0.330**	0.109	-0.159	0.326	0.081	0.178	**-0.469**	0.154
BH	**-0.588**	0.110	**-0.611**	0.333	**-0.471**	0.209	-0.048	0.033
MBW	0.014	**-0.883**	-0.311	**0.378**	-0.112	**-0.311**	0.033	**-0.659**
HLH	-0.122	-0.146	0.256	0.080	**0.559**	-0.250	0.321	**-0.658**
HH	**0.328**	0.152	**0.370**	**-0.390**	-0.137	0.155	0.175	**0.564**
HW	**-0.325**	0.130	**-0.328**	0.014	**-0.320**	**-0.347**	-0.200	-0.108
CPH	0.228	-0.020	**0.408**	-0.110	**0.459**	0.128	**0.409**	0.272
CPW	**1.108**	-0.161	**0.760**	0.304	**0.699**	**0.472**	**0.395**	0.416
DFB	0.090	**0.730**	0.178	-0.022	**0.402**	-0.022	0.262	**-0.612**
DFL	-0.135	**-0.305**	-0.036	**0.604**	-0.243	**0.723**	**-0.418**	-0.175
AFB	-0.152	-0.221	0.081	0.214	0.074	0.259	0.057	0.261
AFL	-0.036	-0.128	-0.280	**-0.607**	**-0.336**	-0.189	**-0.376**	-0.128
CFL	**-0.317**	-0.121	-0.234	0.058	-0.155	-0.147	-0.024	0.127
CFH	-0.011	**0.400**	**-0.432**	0.291	-0.302	**0.436**	-0.238	0.270
PFL	**0.350**	0.029	0.228	**-0.382**	0.128	-0.006	0.166	-0.103
PelvFL	-0.084	-0.124	**-0.379**	0.185	-0.227	0.012	**-0.389**	0.016
Eigenvalue	0.635	0.166	0.554	0.107	0.656	0.277	0.756	0.079
Proportion of total dispersion	0.703	0.184	0.793	0.152	0.619	0.261	0.844	0.088

Traits that distinguish best among treatments are in bold.

Table 6. Summary of morphological traits that characterized specimens reared in the two faster treatments (C and D) from geometric and traditional analyses through the different size classes.

	Geometric analyses		Traditional analyses
Size classes	Lateral	Ventral	
15-20	Slender body Anterior dorsal fin	Narrow mid-body Long caudal peduncle	Long and slender body Narrow and high head Wide caudal peduncle Long pectoral fins Short caudal fin
20-25	Anterior dorsal fin Posterior adipose fin Lower anal fin base position Short anal fin base	Narrow mid-body Long caudal peduncle	Slender body Narrow and high head Wide and high caudal peduncle Small caudal fin height Short pelvic fin
25-30	Long dorsal fin base High caudal region	Long caudal peduncle	Slender body Narrow and long head Wide and high caudal peduncle Long dorsal fin base Short anal fin
30-35	High body Short jaw Long dorsal fin base Anterior anal fin Posterior pelvic fin	Narrow mid-body Long caudal peduncle	Short body Wide and high caudal peduncle Short dorsal fin Short anal fin Short pelvic fins

Traits selected are only based on the first axis of each geometric (CVA) and traditional (DFA) analysis.

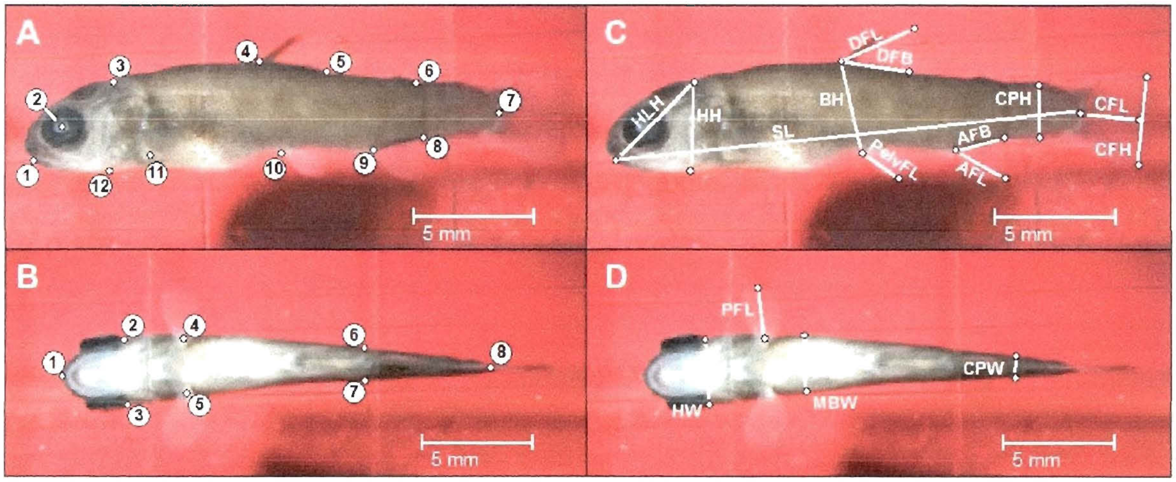

Figure 1. Landmarks and measurements used in morphometric analyses depicted on lateral (A, C) and ventral (B, D) views of *Oncorhynchus mykiss*. All images are from 22 dph fish sampled in treatment A. **A:** Lateral landmarks: 1. Dentary tip. 2. Center of eye 3. Posterior margin of supraoccipital. 4. Anterior insertion of dorsal fin. 5. Posterior insertion of dorsal fin. 6. Posterior insertion of adipose fin. 7. Center of caudal fin. 8. Posterior insertion of anal fin. 9. Anterior insertion of anal fin. 10. Anterior insertion of pelvic fin 11. Anterior insertion of pectoral fin. 12. Lower posterior limit of mandible. **B:** Ventral landmarks: 1. Dentary tip. 2. Posterior limit of left orbit. 3. Posterior limit of right orbit. 4. Left pectoral fin base (at distal radial 3). 5. Right pectoral fin base (at distal radial 3). 6. Left caudal margin (at the anus). 7. Right caudal margin (at the anus). 8. Base of caudal lepidotrichia. **C:** Lateral linear measures: AFB, anal fin base; AFL, anal fin length; BH, body height; CFH, caudal fin height; CFL, caudal fin length; CPH, caudal peduncle height; DFB, dorsal fin base; DFL, dorsal fin length; HH, head height; HLH, head length at head height; PelvFL, pelvic fin length; SL, standard length. **D:** Ventral linear measures: CPW, caudal peduncle width; HW, head width; MBW, maximum body width; PFL, pectoral fin length.

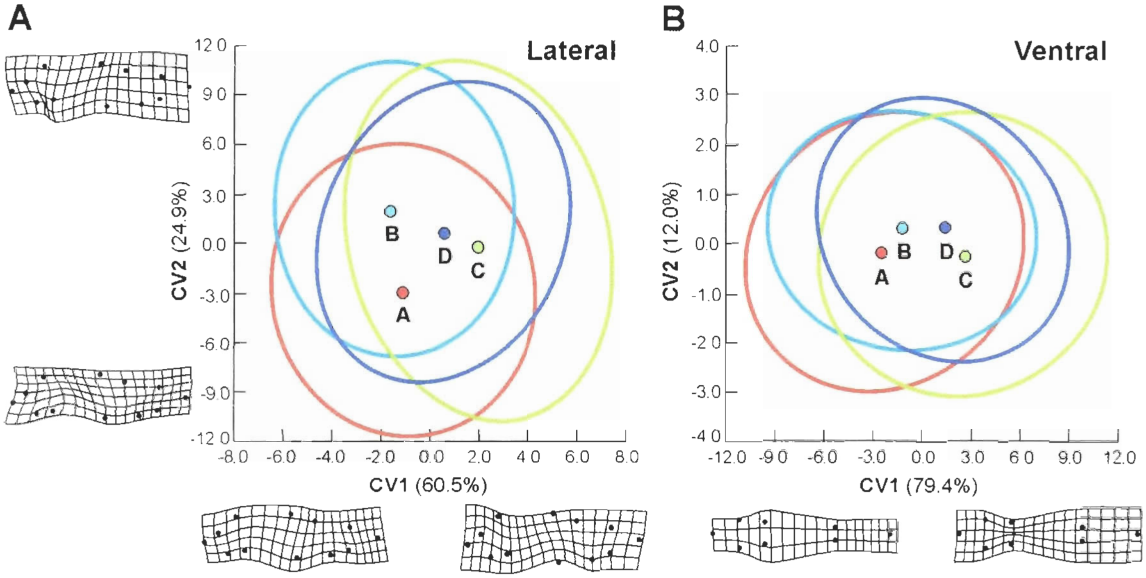

Figure 2. Plots of the first two canonical variates (CVs) among the four velocity treatments (A-B-C-D) of the 15-20 mm size class. Treatment mean scores and the 90% equi-probability ellipses are presented. Deformation grids indicate shape changes from the overall mean associated with each axis. Proportion of total dispersion is indicated on the axis. **A:** Fish lateral view. Two axes were significant for discriminating among treatment means (Axis 1: Wilks' Lambda = 0.594, $P < 0.0001$, Axis 2: Wilks' Lambda = 0.804, $P < 0.01$). **B:** Fish ventral view. Only one axis was significant for discriminating among treatment means (Wilks' Lambda = 0.730, $P < 0.0001$).

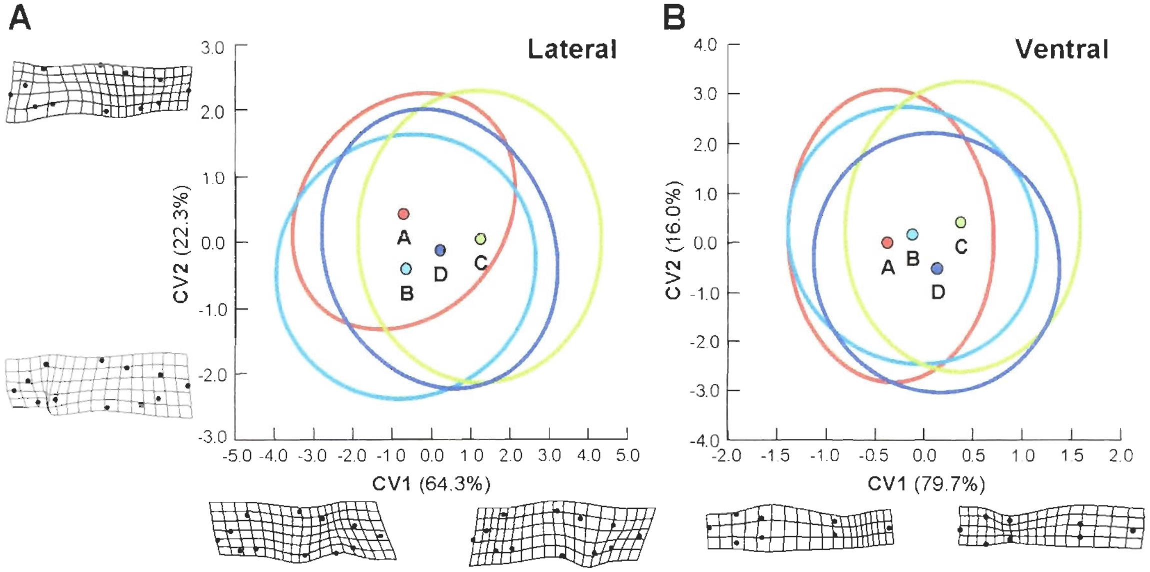

Figure 3. Plots of the first two canonical variates (CVs) among the four velocity treatments (A-B-C-D) of the 20-25 mm size class. Treatment mean scores and the 90% equi-probability ellipses are presented. Deformation grids indicate shape changes from the overall mean associated with each axis. Proportion of total dispersion is indicated on the axis. **A:** Fish lateral view. Two axes were significant for discriminating among treatment means (Axis 1: Wilks' Lambda = 0.649, $P < 0.0001$, Axis 2: Wilks' Lambda = 0.885, $P < 0.05$). **B:** Fish ventral view. Only one axis was significant for discriminating among treatment means (Wilks' Lambda = 0.762, $P < 0.0001$).

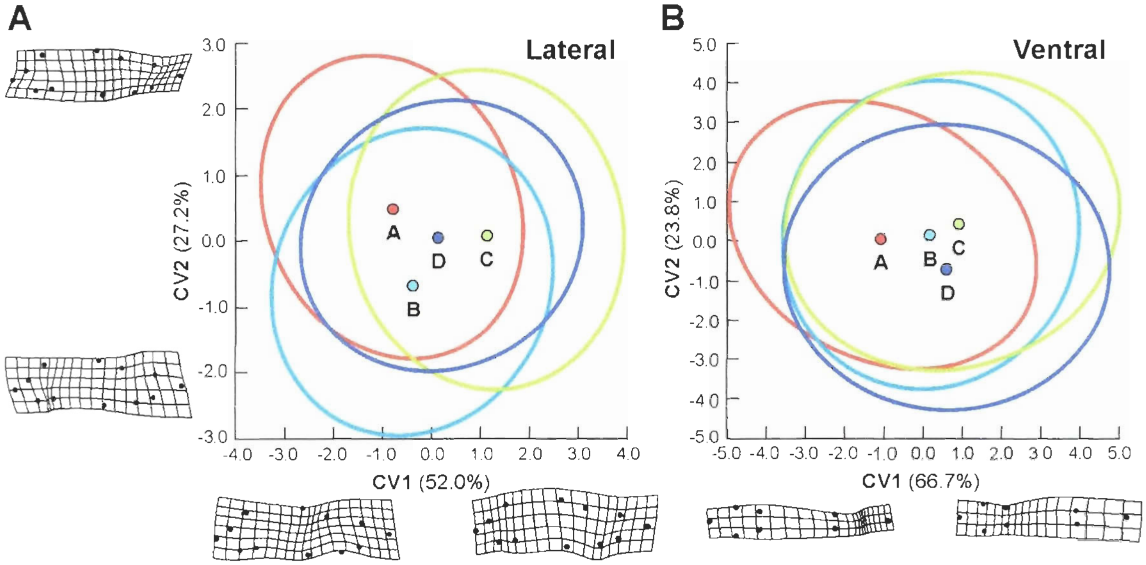

Figure 4. Plots of the first two canonical variates (CVs) among the four velocity treatments (A-B-C-D) of the 25-30 mm size class. Treatment mean scores and the 90% equi-probability ellipses are presented. Deformation grids indicate shape changes from the overall mean associated with each axis. Proportion of total dispersion is indicated on the axis. **A:** Fish lateral view. Two axes were significant for discriminating among treatment means (Axis 1: Wilks' Lambda = 0.581, $P < 0.0001$, Axis 2: Wilks' Lambda = 0.763, $P < 0.0001$). **B:** Fish ventral view. Only one axis was significant for discriminating among treatment means (Wilks' Lambda = 0.798, $P < 0.0001$).

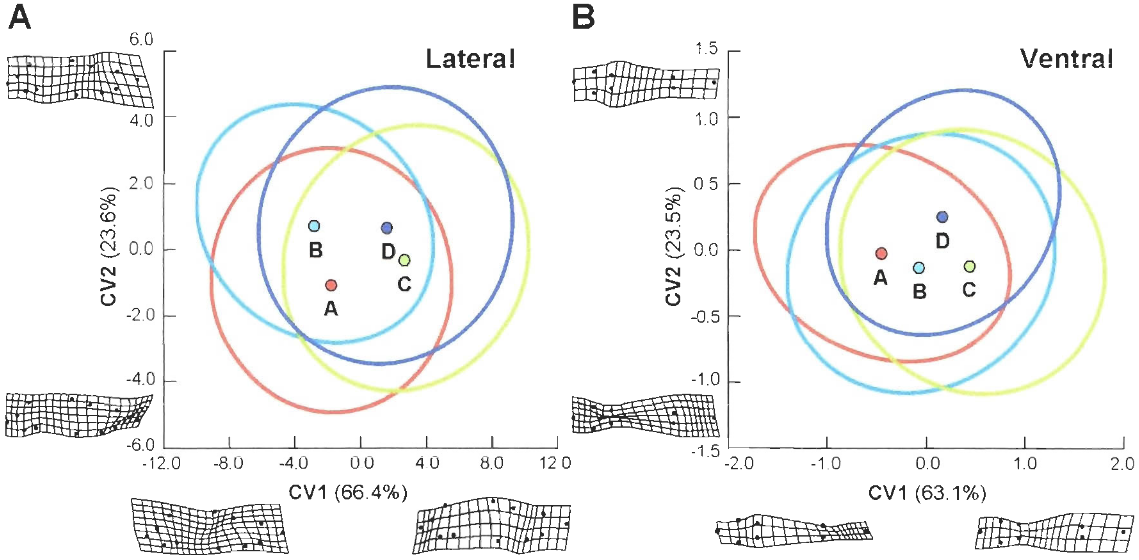

Figure 5. Plots of the first two canonical variates (CVs) among the four velocity treatments (A-B-C-D) of the 30-35 mm size class. Treatment mean scores and the 90% equi-probability ellipses are presented. Deformation grids indicate shape changes from the overall mean associated with each axis. Proportion of total dispersion is indicated on the axis. **A:** Fish lateral view. Two axes were significant for discriminating among treatment means (Axis 1: Wilks' Lambda = 0.543, $P < 0.0001$; Axis 2: Wilks' Lambda = 0.799, $P < 0.01$). **B:** Fish ventral view. Two axes were significant for discriminating among treatment means (Axis 1: Wilks' Lambda = 0.621, $P < 0.0001$; Axis 2: Wilks' Lambda = 0.829, $P < 0.0001$).

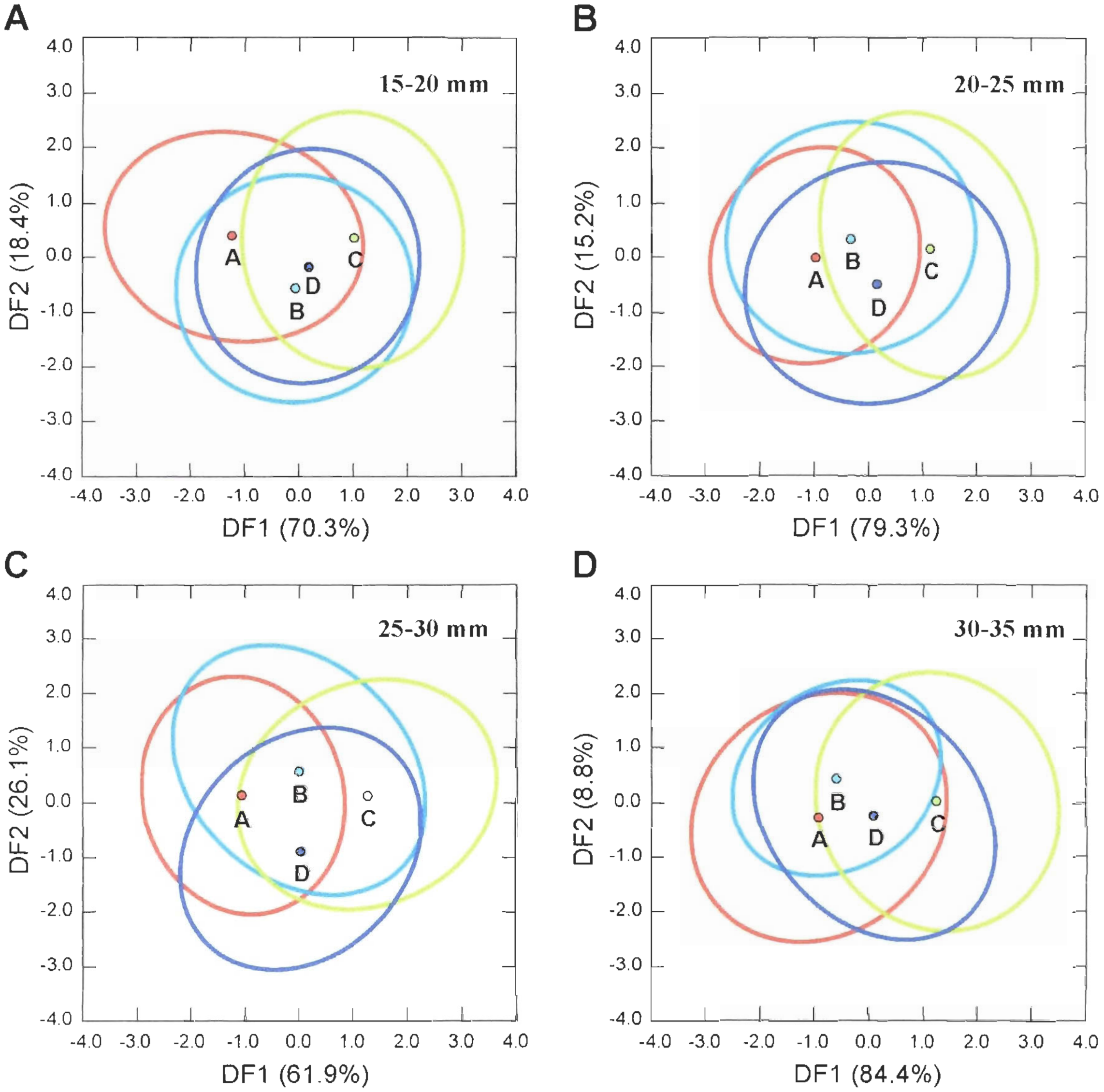

Figure 6. Plots of the first two discriminant functions (DFs) for size adjusted linear distances of each size class. Treatment mean scores and the 90% equi-probability ellipses are presented. Proportion of total dispersion is indicated on the axis. **A:** 15-20 mm. **B:** 20-25 mm. **C:** 25-30 mm. **D:** 30-35 mm.

CONCLUSION GÉNÉRALE ET PERSPECTIVES

La présente étude fournit une description exhaustive de la plasticité morphologique des premiers stades de vie chez la truite arc-en-ciel et utilise de façon complémentaire les méthodes morphométriques traditionnelles et géométriques. Plusieurs points majeurs découlent de ce travail.

D'abord, les variations dans la vélocité du courant entraînent des changements morphologiques à tous les stades de développement étudiés. Ainsi, des différences morphologiques entre les traitements ont été détectées même dès les plus petites classes de taille explorées. Ceci suggère que la plasticité développementale chez la truite arc-en-ciel peut avoir lieu très tôt dans l'ontogénie et qu'elle n'est pas limitée à seulement certaines fenêtres ontogénétiques temporelles.

Ensuite, les modifications induites par la vélocité du courant dans la forme du corps des plus grands poissons ne concordent pas avec les prédictions fonctionnelles établies par les bases hydrodynamiques. Bien au contraire, la forme du corps indique des changements morphologiques inverses aux attentes, sous-entendant une réponse morphologique maladaptative face à la vélocité du courant. En d'autres mots, la forme adoptée par le poisson selon son milieu est, d'un point de vue hydrodynamique, nuisible au poisson.

Comment justifier une telle discordance? Une explication plausible serait que la réponse maladaptive retrouvée dans la morphologie du corps, face à la vélocité du courant, est le sous-produit de la réponse adaptative d'un autre système développemental, soit celle du système musculaire. En effet, dans les vélocités les plus rapides, l'augmentation relative dans la proportion des muscles rouges par rapport aux muscles blancs permettrait d'augmenter les performances durant la nage soutenue des poissons. À l'inverse, dans les milieux à faibles vélocités, l'augmentation de la proportion des muscles blancs permettrait d'atteindre de meilleures performances durant les départs rapides. Cette réponse musculaire entraînerait par conséquent une réponse maladaptative dans la morphologie du corps. Ainsi, il est probable qu'une meilleure performance de nage est obtenue par des changements dans la composition musculaire plutôt que dans la morphologie externe du corps.

Néanmoins, malgré l'impact vraisemblable du développement musculaire sur la forme du corps d'un poisson, aucune raison ne porte à croire que celui-ci peut contraindre d'une quelconque façon la réponse dans la forme et l'arrangement spatial des nageoires. Nos résultats concordent avec ce point de vue, puisque les changements retrouvés dans la forme et la disposition des nageoires dans la plus grande classe de taille concordent avec les prédictions hydrodynamiques. Ainsi, contrairement à la forme du corps, la réponse des nageoires face à la vélocité du courant semble adaptative. Toutefois, il est important de souligner que ces modifications morphologiques ne font qu'au plus suggérer une implication évolutive, puisque les valeurs adaptatives de ces changements n'ont pas été mesurées au cours de cette expérience.

Bien que la plupart des traits morphologiques suivent un même patron de réponse tout au long de l'ontogénie, certains traits exhibent des réponses variables et complexes à travers les classes de taille. Cependant, l'interprétation de ces réponses demeure très difficile puisque les premiers stades de développement des poissons sont des périodes extrêmement dynamiques et changeantes. En effet, les régimes hydrodynamiques (i.e., visqueux, intermédiaires ou d'inertie) et les modes de locomotion employés par le poisson (i.e., anguilliforme ou sub-carangiforme) peuvent varier selon la taille des individus et la vélocité du courant, ce qui, par conséquent, peut influencer la morphologie résultante des alevins. Les données sur les régimes hydrodynamiques et les cinétiques de nage de ces jeunes stades sont nécessaires afin d'interpréter clairement la signification fonctionnelle de ces réponses au cours de l'ontogénie.

Tel qu'exposé dans ce travail, les études ontogénétiques dans la morphologie fonctionnelle procurent une approche puissante pour témoigner des adaptations évolutives des espèces avec leur environnement et pour comprendre les relations entre les changements de forme et de fonction. Le fait que la plasticité d'un être vivant soit multidimensionnelle (i.e., changements potentiels dans la morphologie, la physiologie, le comportement et à différents moments dans le développement) indique que le phénotype peut réagir d'une manière complexe face à des variations abiotiques. Notre étude suggère qu'une même pression de sélection (i.e., vélocité du courant) peut avantager un système (i.e., système musculaire) et nuire à un autre (i.e., morphologie du corps) au cours du développement d'un organisme. Il serait donc intéressant de comparer les réponses morphologiques obtenues dans cette étude avec celles de d'autres systèmes (e.g., musculaire et osseux) face à des variations dans la vélocité de courant au cours des premiers stades de développement de la truite arc-en-ciel.

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