Journal of FISH BIOLOGY

fsbi An International Society for Fish Biology

Journal of Fish Biology (2014) **85**, 1927–1945
doi:10.1111/jfb.12543, available online at wileyonlinelibrary.com

REVIEW PAPER

Maladaptation and phenotypic mismatch in hatchery-reared Atlantic salmon *Salmo salar* released in the wild

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Changes in body shape, fluctuating asymmetry (FA) and crypsis were compared among Atlantic salmon *Salmo salar* fry kept as controls in captivity and those released and subsequently recaptured in the wild according to a before-after-control-impact (BACI) design. Hatchery fish that survived in the wild became more cryptic and displayed a much lower incidence of fin erosion and of asymmetric individuals than control fish kept in captivity. Significant differences in body shape were also apparent, and survivors had longer heads, thicker caudal peduncles and a more streamlined body shape than hatchery controls as early as 20 days following stocking, most likely as a result of phenotypic plasticity and non-random, selective mortality of maladapted phenotypes. Hatchery-reared fish typically perform poorly in the wild and the results of this study indicate that this may be due to phenotypic mismatch, *i.e.* because hatcheries generate fish that are phenotypically mismatched to the natural environment.

Key words: domestication; feralization; hatcheries; phenotypic plasticity; selection; stocking.

INTRODUCTION

Stocking of hatchery-reared juveniles is a common practice in many salmonid conservation programmes. The phenotype of fish, however, can diverge greatly in captivity, and this may affect post-release survival. The question remains about how long it takes for hatchery fish to adapt to the natural environment and for how long hatchery traits persist in the wild. Rearing animals in captivity, free from predators and with a plentiful supply of food, tends to relax natural selection and this can generate individuals with extreme phenotypes that can persist under favourable conditions, but that would have otherwise perished in the wild (Trut *et al.*, 2009). Indeed, as Darwin first noted (Darwin, 1875), one of the defining traits of domesticated organisms is that they tend to exhibit extreme morphological, behavioural and physiological traits rarely seen under natural conditions (Balon, 2004; Teletchea & Fontaine, 2014). For example, hatchery-reared fish often display extreme growth rates (Saikkonen *et al.*, 2011),

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aggression levels (Blanchet *et al.*, 2008), risk-taking behaviour (Roberts *et al.*, 2011) and predator naïvety (Álvarez & Nicieza, 2003) rarely seen among wild fish. Such phenotypic mismatch makes survival of hatchery-reared fish typically low in natural streams (Brown *et al.*, 2003; Jokikokko *et al.*, 2006), and this offers good opportunities for understanding what makes a successful fish: individuals that survive under natural conditions may be expected to be those that are able to adapt most rapidly, or those that resemble wild fish the most (Brown *et al.*, 2003).

Studying adaptive responses in the wild is difficult because the capacity to manipulate phenotypic variation is typically limited (Endler, 1986). Hatcheries, however, can generate large numbers of individuals, some of which will have extreme phenotypes, and if these are released into the natural environment they will probably be exposed to the same selective pressures as wild fish. Thus, monitoring how hatchery fish with contrasting phenotypes fare in the wild could shed light on the nature of selective forces acting upon juvenile fish in general. Feralization, *i.e.* the adaptation of captive-reared animals to natural conditions, may be expected to involve two different processes: (1) selective mortality of maladapted phenotypes (Chittenden *et al.*, 2010), and (2) phenotypic plasticity, *i.e.* the production of alternative phenotypes in response to environmental change (West-Eberhard, 1989) though their relative roles remain unclear.

High phenotypic plasticity is common in many fish (Smith & Skúlason, 1996), and for some migratory species such as Atlantic salmon *Salmo salar* L. 1758 plasticity is probably the consequence of ontogenetic habitat shifts (Von Cramon-Taubadel *et al.*, 2010), which serves to underline the important role that environmental variation has on levels of phenotypic variation of this and other salmonids (Garcia de Leaniz *et al.*, 2007*a*, *b*). For example, body shape variation in juvenile salmonids can be substantial even over small spatial scales, and this is thought to reflect adaptations to local hydrological conditions (Pakkasmaa & Piironen, 2001*a*; Solem & Berg, 2011; Drinan *et al.*, 2012; Stelkens *et al.*, 2012). Indeed, experimentally increasing water velocity tends to produce more streamlined fish (Pakkasmaa & Piironen, 2001*b*). Studies of plasticity in fish have tended to examine phenotypic changes occurring during artificial rearing, and have compared the phenotype of wild and hatchery-reared fish (Kostow, 2004; Von Cramon-Taubadel *et al.*, 2010); studies addressing changes occurring during adaptation to the natural environment are relatively recent (Rogell *et al.*, 2012, 2013; Skaala *et al.*, 2012). Comparisons between wild and hatchery fish can reveal divergence owing to the effects of artificial selection and domestication (Fleming & Einum, 1997; Solem *et al.*, 2006) but results are not always easy to interpret because variation in rearing conditions is typically confounded by maternal effects and genetic origin, and what is being compared are essentially different fish (Garcia de Leaniz *et al.*, 2007*b*). To better understand the responses of fish to changes in rearing environment, a BACI (before-after-control-impact) design (Manly, 2001) is required, so that phenotypic variation can be partitioned into effects due to the environment and effects due to ontogeny. With this approach, the same group of fish (from the same mothers) is compared before and after they are released into the wild, and the influence of natural *v.* artificial conditions can become clearer. Moreover, because survival in hatcheries is typically very high, any phenotypic shifts will be mostly due to phenotypic plasticity, in contrast to natural conditions where changes in trait means will probably be the result of both plasticity and non-random (selective) mortality of some phenotypes. Monitoring changes undergone by hatchery fish in captivity and in the wild, therefore, offers a powerful way

of examining the responses of fish to environmental variation because the differential roles of selection and plasticity can be teased out.

In this study, first-generation hatchery-reared juvenile *S. salar* from a single population were released into four different river environments while a group was kept at the hatchery to serve as a control. Juveniles were then recaptured twice over their first summer and screened at three phenotypic traits shown previously to be related to fitness in salmonids: morphology (Garcia de Leaniz *et al.*, 2007*a*, *b*), fluctuating asymmetry (FA; *i.e.* random deviations from perfect bilateral symmetry; Eriksen *et al.*, 2008) and crypsis (Donnelly & Whoriskey, 1993; Culling *et al.*, 2013). The expectation was that fish released in the wild and subjected to high mortality and large environmental fluctuations would diverge more over time than those kept under more stable hatchery conditions, which would be affected mostly by phenotypic plasticity. It was also expected that different river environments might select for different phenotypes.

MATERIALS AND METHODS

ORIGIN OF FISH

Eighteen anadromous *S. salar* females (mean ± S.D. fork length, L_F, 71·3 ± 7·3 cm) were crossed with 12 anadromous males (mean ± S.D. L_F 68·3 ± 11·0 cm) from the River Taff (South Wales, U.K.) at the Natural Resources Wales, Cynrig Fish Culture Unit (Brecon, Wales) to produce 36 families according to a 1:2 breeding design (whereby milt from a male was added to half the eggs from a female) on 12–19 December 2012. Eggs were incubated under standard hatchery conditions on a flow-through system at ambient temperature (mean ± S.D. 5·83 ± 1·91° C). Families were kept separated until first feeding (30 April 2013) and were then distributed evenly into six 2 m^2 tanks (density *c.* 1·77 $g\,l^{-1}$) and fed at 2·0–3·5% body mass day^{-1} under natural photoperiod (52° N) until late June 2013.

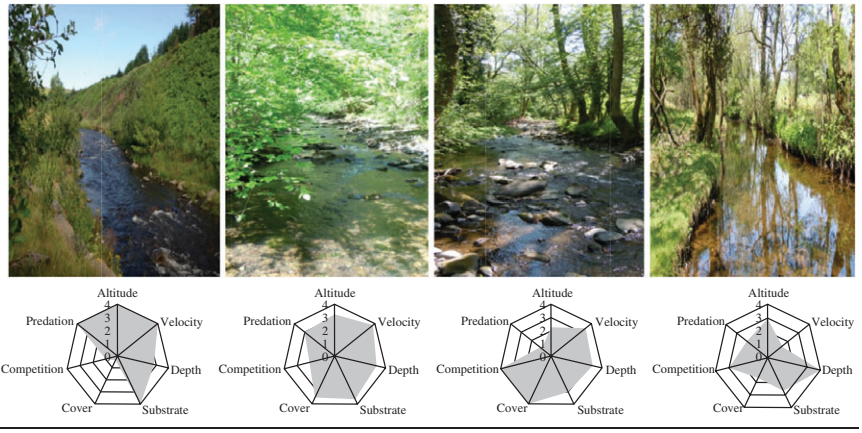
EXPERIMENTAL RELEASES

On 25 June 2013, *S. salar* 0+ fry were accurately hand counted into four groups of 15 000 fish each and transferred into four separate tanks (one per stocking site) to produce 60 000 fish in total. Fish were released along 50 m sections of four first-order stream sites on the headwaters of the River Taff between 27 June and 1 July. Experimental release sites were selected based on the absence of *S. salar* spawning owing to impassable barriers and their location along an altitudinal gradient (from 280 to 153 m above sea level) to maximize environmental variation: Rhondda Fach at Maerdy, River Clydach at St Gwyno Forest, River Dare at Aberdare and River Cynon at Penderyn (Table I). At each site, pH, water temperature (°C), river width (m), water depth (cm), dominant substratum diameter (mm), water velocity ($cm\,s^{-1}$) and extent of vegetation cover (%) were recorded along three evenly spaced transects, one at the downstream end, one midstream and one at the upstream end. Sightings (or markings) of three common fish predators (grey heron *Ardea cinerea*, common kingfisher *Alcedo atthis* and Eurasian otter *Lutra lutra*) were also noted at the time of stocking and at each recapture time to provide an index of predation pressure. As a control group, 300 fish from the same batch of fish were brought to a recirculation system at Swansea University on the day of stocking (time 0), where they were kept under standard hatchery conditions in three 0·65 m diameter × 0·85 m depth circular tanks (stocking density ~ 0·22 $g\,l^{-1}$) and fed 2·5% body mass day^{-1} on commercial fish food under a 14L:10D photoperiod.

RECAPTURE OF STOCKED FISH IN THE FIELD

At each of the four stocking sites, fish were sampled along 6 × 50 m stations (distributed evenly throughout the whole length of the site) using semi-quantitative point electrofishing carried out

TABLE I. Abiotic and biotic characteristics of the four stocking sites on the River Taff, South Wales. Competition and predation were ranked from low to high based on the relative abundance of 0+ *Salmo salar* fry and sightings of aquatic predators relative to the average for the four sites. Sun ray plots show environmental profiles of each site based on seven variables standardized from 0 to 1



Variable	Maerdy	Clydach	Aberdare	Penderyn
Latitude (N)	51·6833°	51·6619°	51·7130°	51·7477°
Longitude (W)	3·4896°	3·3834°	3·4613°	3·4613°
Area (m^2)	6792	6315	5987	5958
Altitude (m)	280	224	153	202
Width (m)	6·86	6·76	5·07	5·70
Water velocity ($m\,s^{-1}$)	0·52	0·49	0·44	0·18
Temperature (°C)	14·7	15·7	16·7	15·3
pH	6·44	6·45	6·40	6·33
Depth (cm)	16·2	18·4	18·2	22·7
Substratum diameter (cm)	16·3	14·7	12·6	10·9
Canopy cover (0–3)	0·22	2·11	2·44	1·00
Competition	Low	Intermediate	High	High
Aquatic predation	High	Intermediate	Low	Low
Avian predators seen	Heron, kingfisher	None	None	Heron, kingfisher
Terrestrial predators	None	None	Otter	None
Stocked previous year	Yes	Yes	No	Yes
CPUE T1–T2)	0·0249–0·0109	0·0238–0·0250	0·0317–0·0249	0·0737–0·0413

CPUE, catch per unit effort; number of 0+ year fry caught m^{-2}. T1, time 1; T2, time 2.

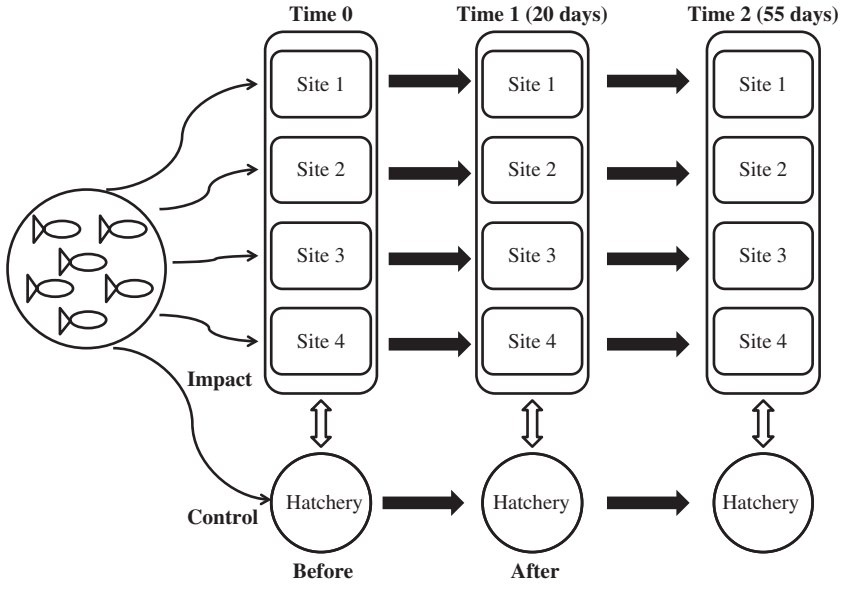


FIG. 1. Before-after-control-impact (BACI) design employed to examine phenotypic shifts undergone by hatchery-reared juvenile *Salmo salar* released into the natural environment. Hatchery fish (control) were stocked into four sites in the wild (impact) and comparisons made before and after release.

from bank to bank in a zig-zag fashion to cover all microhabitats. Sampling was carried out at 20 days post-release (dpr) (15–18 July, time 1) and again at 55 dpr (19–22 August, time 2), and these were compared with the control group kept at the hatchery to conform to a BACI design (Fig. 1). In most cases, 100 fry were sampled per site, except at Maerdy at time 2 where only 70 fry could be recaptured owing to high water level. In each case, *S. salar* recaptures were transported live to the laboratory at Swansea University where they were held in a tank for 24 h to standardize variation in gastric content that could affect measurements of body shape. Measures of crypsis were taken first and then the fish were humanely killed by an overdose of anaesthesia in compliance with U.K legislation. Brown trout *Salmo truta*, L. 1758 and other fish species caught during field sampling were counted to provide an index of interspecific competition and returned live to the river. To provide a reference baseline for the body shape of wild fish, 18 *S. salar* 0+ year fry from the same approximate age (but not derived from stocking) were captured by electrofishing in a tributary in the lower part of the River Taff system (River Rhondda, 51·6043° N; 3·3526° W) on 27 July.

MORPHOMETRIC ANALYSIS

A sample of 90 hatchery fish were randomly selected at the time of stocking to serve as a baseline (time 0). Subsequently, 30 fish from each of the four stocking sites and 30 fish from the hatchery control group (150 in total) were sampled at each time period (time 1 and time 2). For morphometric analysis, fish were photographed (Canon EOS 400D, www.canon.com; 90 mm TAMRON SP Di 1:1 macro, www.tamron.eu/uk) from a fixed distance, facing left and with their fins extended, against a standard background fitted with a scale bar. For each specimen, 19 landmarks used in previous studies (Blanchet *et al.*, 2008; Pulcini *et al.*, 2013) were digitized using the tpsDig 2.16 software (Rohlf, 2010). To correct for possible bias due to body bending, the unbend application of the tpsUtil programme (Rohlf, 2013) was employed, using three additional landmarks along the lateral line to generate corrected landmark co-ordinates (Haas *et al.*, 2010). Co-ordinates were then imported into the software MorphoJ for procrustes superimposition (Klingenberg, 2011), which computes an average shape to which specimens are

aligned in order to remove the effect of size from the study of morphological variation (Vehanen & Huusko, 2011).

Principal component analysis (PCA) was carried out on the covariance matrix followed by separate two-way ANOVA on the first two PCA scores to assess the effects of rearing environment (field *v*. hatchery control) and time on the major features of body shape variation. Phenotypic trajectories of hatchery controls and fish recaptured in the wild were generated by calculating temporal changes in mean PC1 and PC2 along with their 95% C.I. (Adams & Collyer, 2009). Following PCA, discriminant function analysis (DFA) was carried out to quantify the ability to discriminate between hatchery controls and field recaptures at each time point; cross-classification reliability was assessed by using the leave-one-out procedure, and visualized by plots of canonical variate scores at each site and time period.

To assess variation in pectoral-fin length, pectoral fins were digitized separately using ImageJ (Abràmoff *et al.*, 2004) and analysed *via* ANCOVA with L_F as a covariate in $\log_{10}$-transformed values. Opercular and caudal-fin erosion were visually assessed on a scale from 0 (no erosion) to 3 (completely eroded) according to Roberts *et al.* (2011), and comparisons assessed *via* the Mann–Whitney or Kruskal–Wallis tests. The observer was blind to the origin of fish when scoring erosion levels, which have been found to be highly repeatable (Hoyle *et al.*, 2007). Statistical analyses were carried in R 3.0.0 (www.r-project.org).

VARIATION IN CRYPSIS

To quantify variation in crypsis, fish were first placed in individual 25 l white buckets filled to *c.* 10 cm with aerated water and covered with a lid. After 10 min in the white bucket, a photograph (white photo) was taken of each fish against a standard, low-reflectance grey background fitted with a Tiffen Q-13 colour separation guide (www.tiffen.com) and a scale bar, using the same camera and settings as for the morphometric measurements described above. Fry were then transferred to 25 l aerated black buckets, held for another 10 min, and a second photograph (black photo) taken as above. Reflectance values were obtained from each pair of fish photographs (white *v*. black) along three points on each of the three central parr marks of the fish and their corresponding flanks using ImageJ, following the procedure described in Culling *et al.* (2013). Grey-scale calibration was achieved by taking three readings from the white and black Tiffen Q-13 reference colours, and these were then used to derive standardized reflectance values for each fish. Parr mark contrast was defined as the difference between the readings on the parr marks and the flanks, and a crypsis index was calculated as the difference in parr mark contrast between the black and the white photographs taken on the same fish. Two-way ANOVA was used to test for variation in crypsis index and parr-mark contrast with sampling period and fish origin as fixed factors; for parr-mark contrast separate tests were carried out for photographs against white and black backgrounds to avoid pseudoreplication.

FLUCTUATING ASYMMETRY

FA was assessed in relation to three bilateral meristic structures fixed in formaldehyde and viewed under an Olympus SZ40 stereo microscope (www.olympus.co.uk) at ×4 magnification: (1) number of gill rakers in the upper and lower sections of the first gill arch, (2) number of rays in the pectoral fins and (3) number of rays in the pelvic fins. Fin-ray counts were recorded disregarding any branching, scoring only the base of each ray. To test the reliability of the FA scoring, 30 fish were selected with the help of random number generator and meristic counts on each structure were carried out twice in a blind fashion. Repeatability was calculated as the agreement intraclass correlation coefficient (ICC) with the 'psy' R-package, defined as the ratio of the subject variance divided by the sum of the subject variance, the observer variance and the residual variance (Wolak *et al.*, 2012). The proportion of asymmetric individuals for at least one trait was analysed in relation to sampling period and origin of fish as fixed factors by a generalized linear model with a binomial or quasibinomial error structure using R 3.0.0 as by Crawley (2007). The apparent relative mortality of asymmetrical fish in the wild was determined by calculating the proportion of asymmetrical fish that must have died (or emigrated) from the population compared with symmetrical fish that was taken as a baseline equal to one.

RESULTS

PHENOTYPIC TRAJECTORIES AND BODY SHAPE DIVERGENCE

Analysis of phenotypic trajectories *via* PCA plots revealed a marked effect of rearing environment on the body shape of juvenile *S. salar*, resulting in increasing phenotypic divergence of fish in the wild compared with control fish held at the hatchery (Fig. 2). Ontogenetic changes in body shape in the hatchery environment occur mostly along PC2 and result in fish with shorter heads and deeper bodies, whereas changes in body shape in the natural environment occur mostly along PC1 and result in fish with more streamlined bodies and thicker caudal peduncles. Results of ANOVA on PC scores confirm that body shape changes significantly with both time (PC1, $F_{1,333} = 21{\cdot}51$, $P < 0{\cdot}001$; PC2, $F_{1,333} = 18{\cdot}82$, $P < 0{\cdot}001$) and rearing environment (PC1, $F_{1{\cdot}333} = 23{\cdot}19$, $P < 0{\cdot}001$; PC2, $F_{1,333} = 63{\cdot}78$, $P < 0{\cdot}001$); a significant time × rearing environment interaction was found for PC2 ($F_{1,333} = 22{\cdot}87$, $P < 0{\cdot}001$) but not for PC1 ($F_{1,333} = 1{\cdot}29$, $P > 0{\cdot}05$).

BODY SHAPE DISCRIMINATION

Results of DFA are highly significant for all pairwise body-shape comparisons (Fig. 3), and reveal a high discrimination in body shape between hatchery controls and field recaptures (93–97%), as well as between fish sampled at different time periods (87–95%), confirming the results of PC ANOVA. DFA comparisons also indicate that differences in body shape provide good discrimination not only between hatchery controls and wild fish (84%, Hotelling's $T^2 = 805{\cdot}6$, $P < 0{\cdot}001$) but also between wild and stocked fish (100%, Hotelling's $T^2 = 998{\cdot}01$, $P < 0{\cdot}001$). In general, compared to initial baseline values at stocking time, fish kept in the hatchery develop deeper bodies, shorter heads and shorter caudal peduncles over time, whereas almost exactly the opposite occurs when they are released in the wild.

VARIATION IN BODY SHAPE AMONG RELEASE SITES

Plots of the first two canonical variate scores (CV1–CV2) clearly separate hatchery fish from fish released in the wild and, to a lesser extent, also serve to identify fish recaptured in different field sites on the basis of their body shape (Fig. 4). All pairwise DFA comparisons of body shape were significantly different among release sites at $P < 0{\cdot}01$, except between Maerdy and Clydach (first recapture T1, $P > 0{\cdot}05$; second recapture T2, $P > 0{\cdot}05$), with fish stocked in the River Cynon at Penderyn being the ones most different from the rest (Fig. 4).

FIN AND OPERCULA EROSION

Compared with hatchery controls, fish recaptured in the wild had significantly less erosion in the caudal fin (Mann–Whiney, $P < 0{\cdot}001$) and the operculum ($P < 0{\cdot}001$) on both sampling occasions (Table II). Also, unlike in the hatchery, where fish showed no change in caudal-fin erosion ($P > 0{\cdot}05$) or even increased their opercular erosion ($P > 0{\cdot}01$), erosion among stocked fish decreased significantly with time spent in the wild ($P < 0{\cdot}001$). The length of the pectoral fins did not differ significantly between

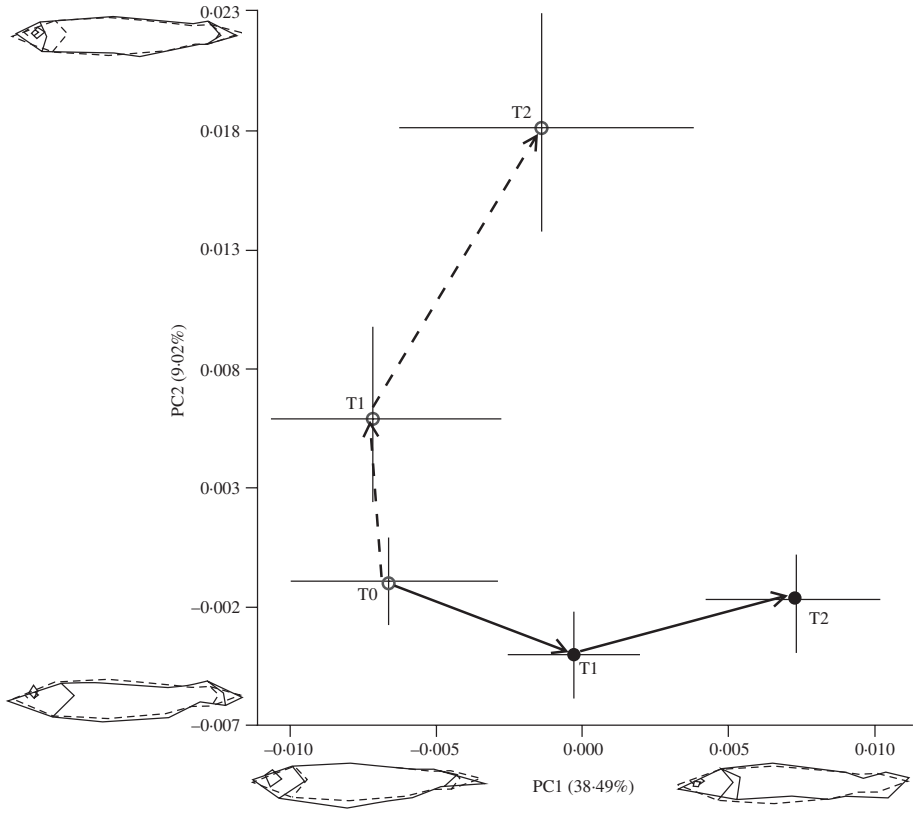


FIG. 2. Phenotypic trajectories in body shape of juvenile *Salmo salar* held at a hatchery as controls (○) or released in the wild (●). Depicted are the means of the first two principal components (PCs; ±95% C.I.) at three sampling times (T0, T1 and T2) during the first 2 months of the first growing season (July to August). Shape variation along each PC is shown by their relative splines at ×2 magnification (___) in comparison to the average body shape (_ _).

hatchery controls and field recaptures while statistically controlling for variation in body size (ANCOVA $F_{1,276} = 3{\cdot}48$, $P > 0{\cdot}05$).

CRYPSIS

Following stocking, parr mark contrast decreased significantly between day 20 and day 55 for both types of fish (time effect; white background $F_{1,92} = 12{\cdot}827$, $P < 0{\cdot}01$; black background $F_{1,92} = 20{\cdot}013$, $P < 0{\cdot}001$) and was always much higher for field recaptures than for hatchery controls, regardless of background colour (origin effect; white background $F_{1,92} = 16{\cdot}000$, $P < 0{\cdot}001$; black background $F_{1,92} = 22{\cdot}735$, $P < 0{\cdot}001$), with interactions being non-significant in both cases ($P > 0{\cdot}1$; Fig. 5). In contrast, variation in crypsis index (*i.e.* the change in parr mark contrast when fish were moved from the white to the black background) did not change between sampling periods ($F_{1,92} = 1{\cdot}250$, $P > 0{\cdot}05$) or differed significantly between hatchery controls and field recaptures ($F_{1,92} = 1{\cdot}076$, $P > 0{\cdot}05$), with the interaction being non-significant ($F_{1,92} = 3{\cdot}400$, $P > 0{\cdot}05$).

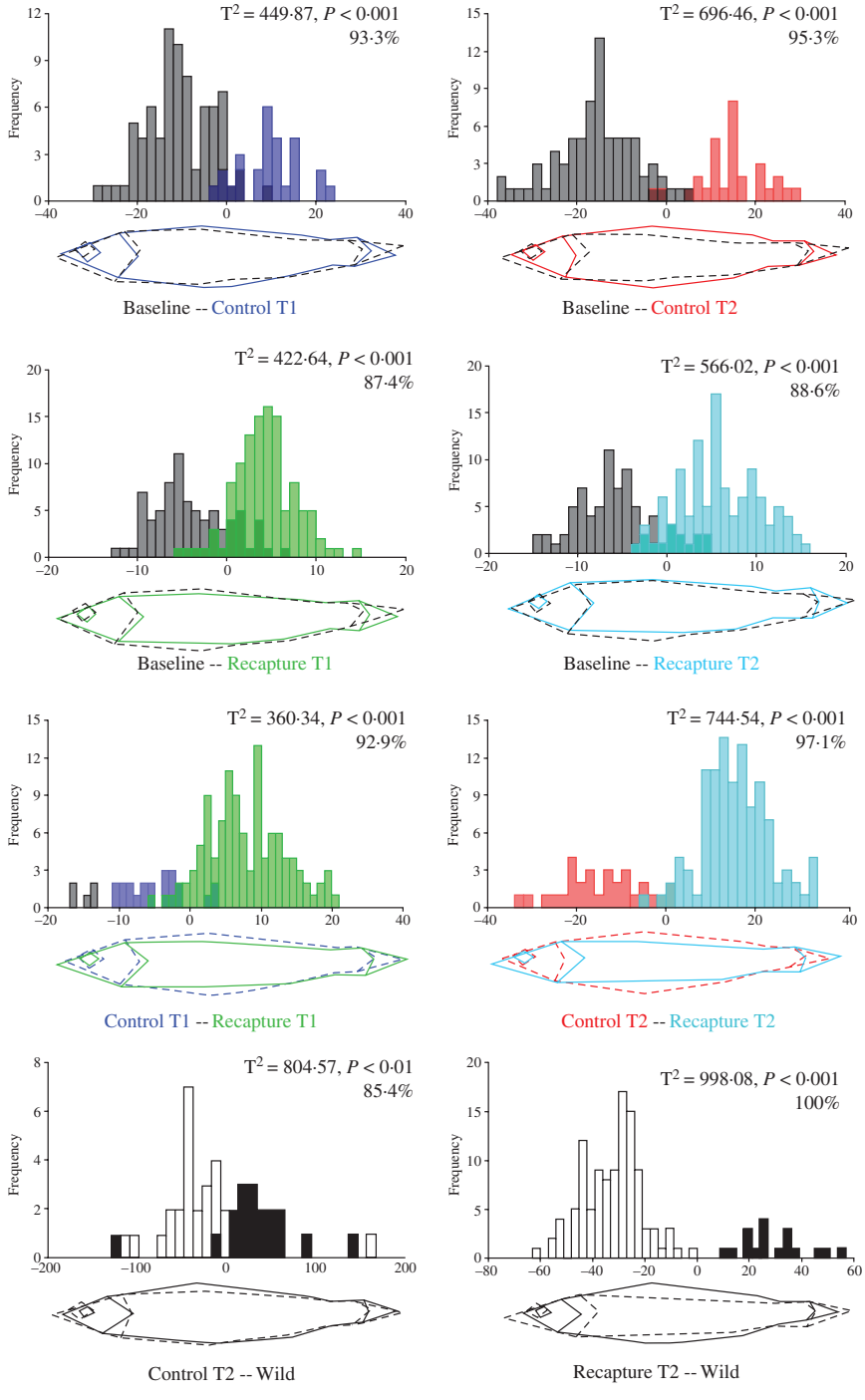


FIG. 3. Discriminant function scores of pairwise comparisons in body shape of juvenile *Salmo salar*, showing leave-one-out % correct classification, Bonferroni-adjusted probabilities associated with Hotelling's T^2 and relative splines (×3 magnification) of body shape change (___) in comparison to the reference shape (_ _).

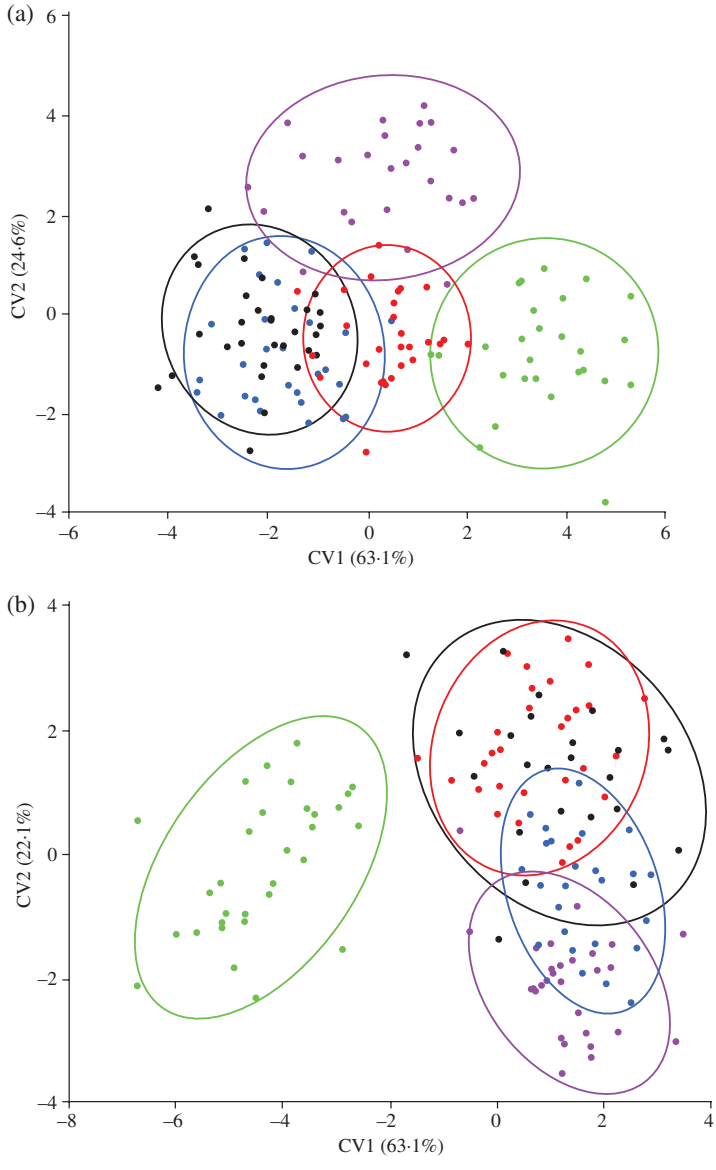


FIG. 4. Canonical variate (CV) plots showing morphometric separation of juvenile *Salmo salar* released at four sites in relation to hatchery controls [hatchery controls (●), Aberdare (●), Clydach (●), Maerdy (●) and Penderyn (●)] at (a) 20 days after stocking and (b) 55 days after stocking.

FLUCTUATING ASYMMETRY AND RELATIVE SURVIVAL OF ASYMMETRIC FISH

Meristic counts on duplicate samples were highly repeatable, as indicated by the very high ICCs (ICC pectoral-fin rays 1·000; pelvic-fin rays 0·998, 95% C.I. = 0·954–1·000; gill rakers 0·988, 95% C.I. = 0·976–0·997). Gill-raker number was the trait with the highest proportion of asymmetrical individuals, followed by number of pectoral-fin

TABLE II. Fork length (L_F), caudal and opercular erosion scores (mean ± S.E.) of hatchery controls and field recaptures at various times since stocking. Associated statistics (Mann–Whitney W or parametric t-test) and significance values are given. Significant pairwise comparisons are indicated in bold.

Trait/Sampling event	Hatchery controls	Field recaptures	Statistic (W or t)	P
L_F (mm)				
Time 0 – stocking	38·25 ± 0·44	37·94 ± 0·51	0·462	>0·05
Time 1 – 20 days	45·86 ± 0·55	44·36 ± 0·44	1·633	>0·05
Time 2 – 55 days	67·31 ± 1·33	51·91 ± 0·51	12·818	**<0·001**
Caudal-fin erosion				
Time 0 – stocking	0·39 ± 0·10	0·41 ± 0·09	718	>0·05
Time 1 – 20 days	0·78 ± 0·14	0·18 ± 0·04	2286·5	**<0·001**
Time 2 – 55 days	0·57 ± 0·09	0·10 ± 0·03	2409·5	**<0·001**
Opercular erosion				
Time 0 – stocking	0·50 ± 0·10	0·51 ± 0·09	722	>0·05
Time 1 – 20 days	0·93 ± 0·09	0·39 ± 0·06	2293·5	**<0·001**
Time 2 – 55 days	0·63 ± 0·09	0·09 ± 0·03	2520·5	**<0·001**

rays and number of pelvic-fin rays (Table III). Most of the fish kept in the hatchery (116 of 134 or 86%) were asymmetrical for at least one of the three meristic traits examined and this percentage remained unchanged over time [Fig. 6(a) and Table III]. In contrast, the per cent of asymmetrical fish in the wild decreased sharply after stocking, and by 55 dpr only 29·9% of individuals (35 of 117) were found to be asymmetrical (binomial 95% C.I. on proportions = 0·218–0·391). Analysis by generalized linear models with binomial errors revealed a significant effect of rearing environment (deviance $G^2_1 = 29{\cdot}19$, $P < 0{\cdot}001$) and time (deviance $G^2_2 = 51{\cdot}09$, $P < 0{\cdot}001$) on the proportion of asymmetrical individuals, as well as a significant interaction time × rearing environment (deviance $G^2_2 = 17{\cdot}37$, $P < 0{\cdot}001$). Given that there was no mortality among hatchery controls over the period of study and that any variation in asymmetry at the hatchery could only be due to sampling error, it was possible to estimate the apparent relative survival of asymmetrical individuals in the wild in relation to that of symmetrical ones. The results [Fig. 6(b)] indicate that the relative survival of asymmetrical fish was 53% of the survival of symmetrical fish 20 dpr (binomial 95% C.I. = 43·3–63·6) and dropped to only 8·5% at 55 dpr (binomial 95% C.I. = 3·6–15·4).

DISCUSSION

This study employed a BACI approach to investigate how the morphology, crypsis and FA of juvenile *S. salar* change when hatchery-reared fish are released into the wild, providing in this way an assessment of the process of fish feralization, *i.e.* the adaptation of fish to the natural environment or the process of domestication in reverse (Price, 2002; Zeder, 2012).

The phenotype of *S. salar* fry changed substantially over time, and fish in the wild diverged significantly from hatchery fish as early as 20 dpr. Compared with hatchery controls, juvenile *S. salar* in the wild became more streamlined, more symmetrical, developed longer heads, thicker caudal peduncles, and their caudal fins and opercula

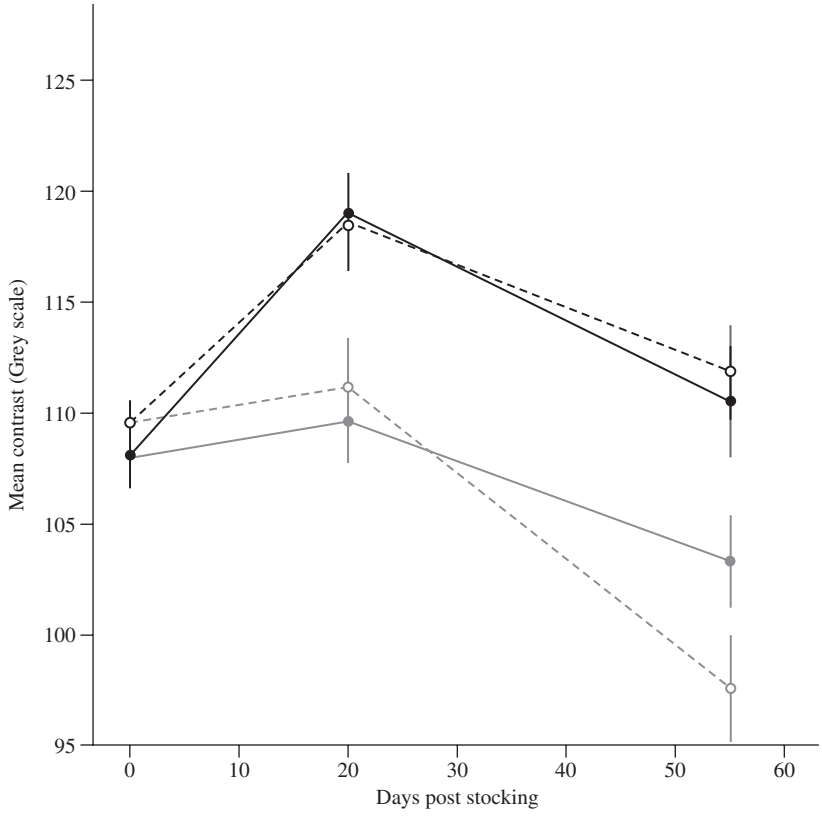


FIG. 5. Variation in mean ± S.E. parr mark contrast of hatchery controls (○) and field recaptures (●) after being kept for 10 min in a white (– –) or black (——) container.

regenerated. The fitness implications of such phenotypic changes are difficult to predict in the wild but are likely to be adaptive because morphology affects swimming efficiency (Pakkasmaa & Piironen, 2001*a*, *b*), feeding ability (Adams *et al.*, 2003) and predator avoidance (Drinan *et al.*, 2012). For example, streamlining of body shape and head length has been demonstrated in salmonids reared in fast water (Pakkasmaa & Piironen, 2001*b*) and is thought to reduce drag and swimming costs (Enders *et al.*, 2004), making foraging more energetically efficient (Pakkasmaa & Piironen, 2001*a*; Vehanen & Huusko, 2011; Drinan *et al.*, 2012). Head length, body depth and fin size are the characters that best discriminate among juvenile *S. salar* from different rivers in Norway (Solem & Berg, 2011) and variation in these is thought to reflect adaptations to local conditions in *S. salar* (Garcia de Leaniz *et al.*, 2007*a*, *b*). Confinement in hatchery tanks with low water velocity and plentiful food increases fat deposition and results in deepening of the body amongst hatchery-reared salmonids (Pulcini *et al.*, 2014), and this was also evident in this study. Similar changes have been reported for other fish species and serve to highlight the different selective pressures that fish experience in natural and artificial environments (Lorenzen *et al.*, 2012), and the strong effects that food regime and swimming activity can have on fish body shape (Pakkasmaa & Piironen, 2001*b*; Marcil *et al.*, 2006).

TABLE III. Proportion of asymmetric individuals for three meristic traits (95% binomial C.I.) at various sampling times

Trait	Baseline – T0	T1 – 20 days	T2 – 55 days
Pectoral-fin rays			
Hatchery controls	0·57 (0·41–0·71)	0·31 (0·11–0·58)	0·29 (0·10–0·55)
Field recaptures	0·60 (0·43–0·75)	0·28 (0·18–0·39)	0·07 (0·02–0·15)
Pelvic-fin rays			
Hatchery controls	0·48 (0·30–0·67)	0·22 (0·09–0·42)	0·21 (0·08–0·41)
Field recaptures	0·49 (0·32–0·65)	0·30 (0·22–0·40)	0·10 (0·05–0·17)
Gill rakers			
Hatchery controls	0·82 (0·68–0·92)	0·67 (0·47–0·83)	0·48 (0·30–0·68)
Field recaptures	0·72 (0·56–0·85)	0·59 (0·50–0·68)	0·14 (0·09–0·22)

Pectoral fins are important for station holding in juvenile *S. salar* as they act as hydrofoils, generating downward force and allowing fish to occupy high-velocity feeding stations (Armstrong *et al.*, 2003; Drinan *et al.*, 2012). Fin and opercular erosion are a common problem in hatchery-reared salmonids (Bosakowski & Wagner, 1994; Latremouille, 2003), which tend to have shorter fins than wild fish (Blanchet *et al.*, 2008). This was also the case in this study with respect to opercular and caudal-fin erosion, which may have affected the swimming ability of stocked fish, though no difference was found for pectoral-fin length. The fact that erosion decreased with time in the wild, but increased in the hatchery, probably reflects some regeneration under natural conditions and is also consistent with selection against maladapted phenotypes, in this case against fish with shorter than average tails and shorter than average opercula. The latter is also suggested by changes in body shape, which revealed an enlargement of head length in the wild and a shortening in the hatchery, likely as a result of opercular erosion.

Fry in the wild also displayed darker parr marks than hatchery controls, and this would have made them more cryptic and less conspicuous to predators (Donnelly & Dill, 1984; Donnelly, 1985; Donnelly & Whoriskey, 1993; Culling *et al.*, 2013). Salmonids show considerable plasticity in parr mark pigmentation that depends on diet, and also responds to a number of environmental variables including water transparency and substratum type, which is likely to be under selection (Culling *et al.*, 2013). Colour change in salmonids can occur rapidly (Westley *et al.*, 2013) and this study found significant differences in parr mark contrast within just 20 days. The low parr mark contrast displayed by hatchery controls is typical of slow-flow, low-gradient environments (*i.e.* pools) with homogeneous backgrounds (Donnelly & Dill, 1984), which characterize hatchery tanks. Moving fish from a light to a dark background had no consistent effect on the crypsis index in this study, which was unrelated to sampling period or fish origin. The ability to change colour instantly, termed physiological colour change (Westley *et al.*, 2013), may require longer acclimatization periods than the 10 min used in this study. This is similar to the findings of Donnelly & Whoriskey (1993) who reported that juvenile *S. salar* acclimatized to a light background were unable to camouflage to a darker background in order to avoid predation.

Under stabilizing selection, feralization may be expected to result in phenotypic convergence by selecting some optima on behaviours and body plan (Zeder, 2012) but this

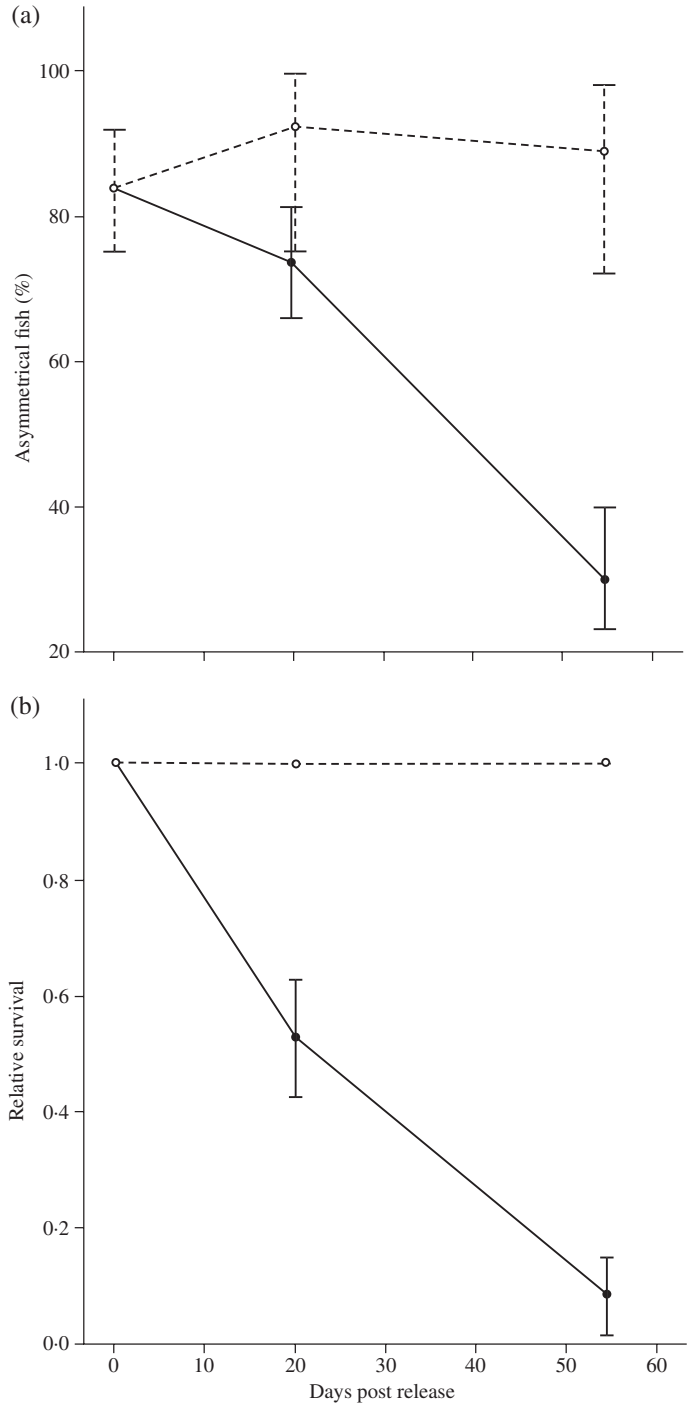


FIG. 6. Temporal change in (a) per cent juvenile *Salmo salar* that are asymmetric for at least one meristic trait (± binomial 95% C.I.) amongst hatchery controls (○) and field recaptures (●), and (b) apparent relative survival (± binomial 95% C.I.) of asymmetrical fish (●) in relation to baseline for symmetrical fish (○).

was not the case in this study. Juvenile *S. salar* stocked in the wild strongly diverged from hatchery fish with increasing time spent in the wild but did not appear to converge towards the body shape of wild fish, which remained morphologically differentiated from both hatchery controls and stocked fish. Although the sample of wild fish is admittedly small, these results serve to highlight that morphometric comparisons also need to consider potential differences in genetic background, that phenotypic variation in juvenile *S. salar* is probably the norm and that there may not be just one single body plan optimal for all environments. Fish released at different sites had statistically different (albeit only slightly) body shapes at recapture, and recaptured fish were not more similar to wild fish than hatchery fish were. There was some phenotypic divergence among the four field sites and some evidence that these may have been related to the environment fish lived in. Thus, fish released at Penderyn developed the most distinct body shape. As this site is characterized by having the slowest water velocity, the deepest water, the smallest substratum and the greatest extent of pool habitat, it is tempting to speculate on a relationship between river habitat and body shape. *Salmo salar* fry prefer shallow riffles with water velocity between 20 and 40 cm s^{-1} and avoid slow-flowing waters with velocities <5–15 cm s^{-1} (Armstrong *et al.*, 2003). Penderyn had an average velocity of 18 cm s^{-1}, so it may not have been an ideal habitat for *S. salar* fry. Studies in other species have found that fish can respond rapidly to slow flows by developing deeper bodies and smaller heads (Haas *et al.*, 2010) and this may have also been the case at Penderyn.

Taken together, the phenotypic shifts observed among *S. salar* fry in the wild are likely to be adaptive because the traits involved are related to fitness in salmonids (Garcia de Leaniz *et al.*, 2007*a*, *b*), and the nature of the changes was in the expected direction. Yet, the extent to which these were the result of phenotypic plasticity or non-random mortality (or emigration) of maladapted phenotypes is unclear. Given that there was no mortality in the hatchery, two different mechanisms must have been at work: phenotypic plasticity in the hatchery, and plasticity plus selection in the wild. Consideration of FA as an index of development instability, *i.e.* the inability by an embryo to produce a consistent phenotype in a given environment (Johnson *et al.*, 2004), may shed some light on the relative importance of plasticity and selection. The development of bilateral structures on opposite sides of an organism (such as pectoral fins) is controlled by the same genes, and any deviations from perfect bilateral symmetry are thought to result from environmental and genetic stressors (Johnson *et al.*, 2004). High levels of FA in some hatchery stocks (Vøllestad & Hindar, 1997; Yurtseva *et al.*, 2010) have been linked to maternal stress, environmental fluctuations during embryo development and reduced genetic variation (Leary *et al.*, 1985*a*, *b*), though a general relationship linking FA and heterozygosity appears only weak (Vøllestad *et al.*, 1999). In this study, the per cent of asymmetrical individuals remained high at 86% in the hatchery and did not change over time, but decreased sharply in the wild, and by day 55 only 30% of field recaptures were asymmetrical. As the meristic structures considered are not plastic but become fixed instead during early development (Swain & Foote, 1999; Yurtseva *et al.*, 2010), the observed decrease in the frequency of asymmetrical individuals in the wild must have been due to a higher mortality (or emigration) of asymmetrical fish relative to symmetrical ones. To generate the observed results, it was estimated that asymmetrical fish must have been *c.* 12 times more likely to die or emigrate from the study area than symmetrical fish. Given that the frequency of asymmetrical individuals can be up to four times higher among hatchery fish than among

wild fish (Crozier, 1997; Moran *et al.*, 1997; Vøllestad & Hindar, 1997), much of the phenotypic changes in this study must therefore be attributed to non-random mortality (or emigration) of maladapted hatchery phenotypes and not simply to plasticity.

A significant decrease in FA with time has been reported previously for wild *S. salar* by Moran *et al.* (1997), who noted that such changes did not occur in captivity, and who suggested a role for natural selection in the purging of asymmetrical individuals from wild populations. Several authors have also found a positive association between FA and environmental stress in fish (Allenbach, 2011), as well as a decrease of FA with fish age, which is suggestive of non-random mortality of asymmetrical fish and, therefore, of selection (Sánchez-Galán *et al.*, 1998). Comparison of different meristic structures indicates that the highest incidence of asymmetrical individuals was found for the number of gill rakers, followed by number of pectoral-fin rays and by the number of pelvic-fin rays, in agreement with previous studies on *S. salar* (Crozier, 1997). In general, field recaptures were two to four times more symmetrical than hatchery controls, depending on the structure, but the extent to which FA for individual traits can be related to their effect on fitness remains unclear (Moran *et al.*, 1997; Vøllestad & Hindar, 1997).

A link between form and function is assumed to exist in the body shape of fish (Thompson & Bonner, 1961) and natural selection may be expected to favour those phenotypes that increase fitness in local environments (Solem *et al.*, 2006). Hatchery-reared fish typically perform poorly in the wild (Munakata *et al.*, 2000; Jokikokko *et al.*, 2006) and the results of this study suggest that this may be due to phenotypic mismatch, *i.e.* because hatcheries generate fish that are phenotypically mismatched to the natural environment.

We are grateful to a number of Swansea University volunteers and to staff at Natural Resources Wales for rearing the fish at Cynrig and for help with the sampling in the River Taff. This work was in part funded by the European Social Fund (ESF) through the European Union's Convergence programme administered by the Welsh Government.

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