Comaparing anadromous brown trout in small, neighbouring catchments across contrasting landscapes: what is the role of environment in determining life-history characteristics?

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Running Head: Orkney *S. trutta* across landscapes

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Abstract

Study of anadromous brown trout in Orkney burns (small streams) with a common-garden sea in Scapa Flow supports the key role of nutrient availability in fresh water, independent of day length, as a determinant of smolt age, with a systematic increase in mean smolt age from 1 to 3 years related inversely to productivity. Whole catchment (8 km^2) population budgets indicated annual smolt production of around 650 from approximately 100 spawners. Egg to smolt survival was 0.65 %, while marine survival was estimated from mark recapture to be between 3.5 and 10 %. The question of B-type growth (accelerated growth immediately prior to or during smolt migration) was also addressed, with a strong negative correlation between B-type growth and size at end of winter suggesting that this represents a freshwater compensatory growth response,. The data obtained indicate the potential importance of small catchments for supporting anadromous *Salmo trutta* populations and suggest that small runs of spawners (< 100 individuals) are adequate to maintain stocks in such situations. They also support the key role of freshwater productivity in determining life-history characteristics over small spatial scales, with Orkney providing a useful natural laboratory for future research into metapopulation genetic structuring and environmental factors at a tractable scale.

Key words: B-type growth; cohort analysis; Orkney; *Salmo trutta*; sea trout; smolt age.

INTRODUCTION

Anadromous brown trout *Salmo trutta* L. 1758 (also known as sea trout) have long been recognized as an important resource (Elliot, 1989), but understanding of their biology has been hampered by problems of large river catchments, sympatry with Atlantic salmon *S. salar* L.1758, complex relationships with riverine and lacustrine resident *S. trutta* populations, as well as confounding of latitudinal variation in population characteristics with geological, and hence trophic, factors. Anadromous *S. trutta* have shown a general trend of decline across their range over several decades (ICES, 2013). This decline, which has paralleled that seen in *S. salar* (Chaput, 2012), has stimulated research into their biology, but has also highlighted that several aspects of their ecology remain poorly understood (Harris & Milner, 2006). Consequently, a number of key research themes have been identified (Milner *et al.*, 2006a), including, amongst others: comparative study of stock-and life history strategies across a wide range of stream types; information underpinning management of smaller rivers, which provide important spawning and nursery habitat for anadromous *S. trutta*, but not *S. salar*; more research into environmental controls on the migratory habit.

Little research is available on the biology of anadromous *S. trutta* in small rivers (maximum channel width < 6 m) although *S. trutta* are more abundant *than S. salar* in such rivers (Milner *et al*., 2006b). Most previous studies of small streams have focussed on either a single catchment (Mortensen, 1977; Rubin *et al*., 2004; Ayllon *et al*., 2006) or relatively widely spaced streams (Jonsson *et al*. 2001). An exception was the work of Laikre *et al*. (2002), that examined genetic relationships across 13 streams on the Baltic island of Gotland, although ecological and life-history variation across catchments were not considered.

A key issue in sea trout life-history is what factors influence the smolting age. Previous work has focussed largely on latitudinal clines in mean smolt age (Jonsson & L'Abée-Lund, 1993; Jonsson *et al*., 2001), which may be confounded with decreases in river productivity with increasing latitude (at least from around 40ºN; Gross *et al*., 1988). The problem in unpicking environment from latitudinal variables such as photoperiod and growing season length is a lack of anadromous *S. trutta* rivers in close proximity but with markedly different productivity alongside demonstrably similar marine conditions. A further complication is the need to characterise the degree of migration in the trout population, necessitating extensive sampling which is not usually possible in larger catchments.

Another question which has rarely been addressed in the anadromous *S. trutta* literature is the phenomenon of so-called B-type growth [accelerated growth prior to or during the smolt migration (Went, 1938, 1949; Fahy, 1990), also referred to as spring (Heidarsson *et al*., 2006) or run-out (Poole, 2011) growth] and in particular its relationship with freshwater environmental conditions, smolt age and transition to marine conditions. B-type smolts, which exhibit such growth, are contrasted against A-type smolts, which migrate without any growth beyond the last annulus (Went, 1938; Thomson, 2015). An association of B-type growth with smolt age might help to reconcile views on whether there is a threshold size for migration, [supported by Fahy (1990), rejected by Økland *et al*. (2003)] and how this relates to other environmental conditions.

The present paper addresses the themes selected above from Milner et al. (2006a) through examination of anadromous *S. trutta* populations in the Orkney Islands, off northern Scotland, U.K. The nature of Orkney's environment, especially around the enclosed marine basin of Scapa Flow (Fig 1), provides an excellent situation for detailed study of anadromous *S. trutta* compared to larger systems elsewhere. The small size of Orkney burns (streams) eases sampling of their trout populations over short timescales, whilst it also means that *S. salar* are absent (Thomson 2015), thus simplifying analyses. More importantly, the existence of numerous anadromous *S. trutta* populations across contrasting habitats in a confined region with a common-garden sea means that effects of latitude (Jonsson & L'Abée-Lund, 1993; Jonsson *et al*., 2001) and marine variation can be removed as influences, facilitating clearer assessment of other parameters such as temperature, land-use and stream size. Similarly, the complication of lacustrine features is removed in Orkney burns, as most have none.

The aim of the present work was to sample anadromous *S. trutta* populations from contrasting burns around Scapa Flow to address the following questions, relating to the themes identified above. Can a robust cohort assessment be made of a burn system to allow evaluation of survival through the life cycle and assessment of egg deposition? Do life-history characteristics, specifically smolt age, differ between contrasting catchments? How does B-type (run-out) growth relate to seaward migration in very short burn systems?

MATERIALS & METHODS

STUDY SITES

Previous work (Thomson 2015) identified catchments in Orkney supporting populations of anadromous *S. trutta*. Four of these, which discharge into Scapa Flow, were selected for more intensive study because of their contrasting characteristics (Fig. 1 and Table I). Two catchments (Whaness and Ore Burns) were on the island of Hoy, which is characterized by peatland and heather moorland (Land Use Consultants, 1998), meaning that they are relatively oligotrophic. Ore Burn has a simple single stem structure without major tributaries, but a relatively high discharge (Table I). Whaness Burn has a single tributary, but lower discharge (Table I). The other two catchments (Eyrland and Bu Burns) were on the Orkney Mainland. Burn of Eyrland is the largest non-lacustrine catchment in Orkney (Table I). It rises on heather moorland but then flows through improved grazing land over much of its length. Bu Burn is short (Table I) and comprises a single stem with no significant tributaries, flowing entirely through grazing land. Both Mainland burns rise at a similar altitude (140 m) and are relatively eutrophic, Bu Burn more so than Eyrland (authors, pers. obs.). Between the four catchments there are thus contrasts between structure, nutrient status, altitude and discharge, but all have a common marine environment in Scapa Flow.

ELECTROFISHING

Samples of *S. trutta* juveniles, smolts and mature resident trout were caught using a WFC 911 backpack electrofishing set (Electracatch International Ltd; www.electracatch.com). The unit comprised re-chargeable 24 V batteries generating

0-400 V smoothed DC. Electrofishing protocols followed those of the Scottish Fisheries Co-ordination Centre (SFCC, 2007). All surveys involved two people, one using the electrofishing equipment, the other with a hand net and bucket to retain the catch. After a brief test, to adjust the voltage, fishing was in an upstream direction, the anode being moved side-to-side ensuring coverage across the entire burn width. Voltage was 150 V, unless larger trout were expected, when lower settings were used.

Single run, 10 min timed surveys were used for rapid semi-quantitative assessments without use of stop nets. The wet area fished (length and width at 8-10 points for each site) was recorded to allow calculation of catch per unit effort (CPUE) data (fish m^{-2}), which enabled comparison between catchments and years.

TRAPPING

Downstream (2007-2010) and upstream (2007 and 2009) fish traps were installed in the Burn of Eyrland (Fig. 1) to sample downstream migrating smolts in spring and upstream spawners in autumn. The presence of a dam and fish ladder a short distance from the sea made this the best site for these installations.

Downstream trap

The smolt (downstream) trap was installed each spring between 2007 and 2010 in the form of an inclined plane or “Wolf” trap (Wolf, 1951). This involved blocking the fish ladder and channelling water over the dam and through a set of screens extending 1.2 m from the dam lip and sloping (20°) downwards. The spacing of the screen bars was 10 – 11 mm. An irrigated plastic trough, perpendicular to the water flow along the bottom of the screens, led via a short pipe to a lidded holding box.

Upstream trap

The trap was installed in the pool upstream of the dam, directly above the upstream exit from the fish ladder, so that all fish ascending the ladder swam directly into it. Anadromous *S. trutta* were unable to ascend the dam directly owing to insufficient water-depth downstream to negotiate its height. The trap comprised a timber-frame box, measuring 160 x 80 x 60cm, walled with 2.5 cm mesh galvanised steel. The entrance to the box was either a net eye, taken from a fyke net (2007) or a V-shaped channel constructed from 2.5 cm mesh galvanised steel (2009). These structures prevented fish from exiting back down the fish ladder. The box was secured with ropes and weights. The trap operated mid-September to mid-December (2007) or mid-August to early December, (2009), in both cases encompassing the entire run. It was checked daily each morning, with additional visits during the main sea trout run and periods of high flow.

Fish processing

After capture, all fish were anaesthetized [2-phenoxyethanol (Sigma, UK), 0.5 ml/l] in small batches (parr and smolts) or individually (adults) to allow weighing (Mettler Digital Battery Scale; www.mt.com), length measurement, scale sampling and, for smolts only, visible implant (VI) tagging (Northwest Marine Technology Ltd.; www.nmt.us), adipose fin-clipping of all VI tagged fish and classification of smolting status (Table II). Fish were placed in a bucket of clean water where they recovered within 2 min. They were then carefully released back into the watercourse. Scale samples were retained in individually labelled paper packets for later reading.

Downstream Trap Efficiency

A sub-sample of smolts was tagged and released upstream of the trap. Efficiency was calculated as the percentage of marked smolts recaptured as they repeated their downstream movement through the trap, including any which were captured the following year. The mean trap efficiency calculated across 2008 and 2009 was 72.8 %.

COHORT ANALYSIS FOR BURN OF EYRLAND

Scale reading was done using a Zeiss Axiostar compound microscope (40x magnification; www.zeiss.com) with a mounted digital camera (9 MP resolution) to record images of all scales. Scale reading and fish-size back-calculation followed the method of Elliott & Chambers (1996). Estimation of egg deposition was based on fecundity data for anadromous *S. trutta* (Solomon 1997), along with median length and number of returning females recorded in 2007. Such individuals were distinguished from males by their lack of facial remodeling (kype formation) and lack of milt expression. The short length and small size of this burn meant that anadromous *S. trutta* entering from the sea were on the point of spawning, so that these characteristics were considered an accurate indicator of sex ratio. Numbers of 0+ year fish were determined the autumn after spawners had returned (2008) by electrofishing survey at 9 sites. Area fished, stream length and median width were combined to give a total population estimate. Numbers of age 1+ years and older fish were similarly surveyed in autumn 2009, and smolt production estimated from downstream trapping in the spring of 2010 corrected by application of the mean trap efficiency.

SMOLT AGES ACROSS CATCHMENTS

Scale reading was performed as above, from samples obtained from electrofishing during the smolt run (all catchments) or from trapping (Eyrland only).Smolt ages were determined from the number of annuli visible on the scales of each individual, and the median smolt age calculated for each catchment.

ANALYSIS OF B-TYPE GROWTH

Scale reading was performed as above. B-type growth was identified in smolts captured during the smolt runs in all four catchments either from electrofishing or downstream trap samples, as above. B-type growth was visible as wider-spaced circuli at the scale edge, contrasting with closely spaced circuli in the preceding winter growth annulus (Went, 1962; Fig. 2). The extent of B-type growth was measured from the last winter annulus to the scale edge, and used to back-calculate (Elliot & Chambers, 1996) the equivalent length change attributable to B-type growth in each individual. Fork length back-calculated at the last annulus (calculated fork length, L_{Fc}) was also noted and used to assess the extent to which size at end of winter prior to migration determined B-type growth.

STATISTICAL ANALYSES

The relationship between L_{Fc} at the last annulus and B-type growth was analysed using Pearson's correlation analysis, whereas comparisons between B-type growth in smolting *versus* non-smolting *S. trutta* were made using one-way ANOVA and Fishers lowest significant difference (LSD) *post hoc* test. All analyses were done using SPSS version 16 (SPSS Inc.; www.ibm.com), with significance accepted at probabilities of 0.05 or less.

RESULTS

COHORT ANALYSIS FOR BURN OF EYRLAND

The median size of returning female anadromous *S. trutta* (n = 51) in autumn 2007 was 45 cm. Using Soloman's (1997) mean line for British anadromous S. trutta fecundity gave an estimated egg abundance of 88 170 (Fig. 3). The following autumn (2008), the population of 0+ year *S. trutta* in Burn of Eyrland catchment was estimated to be 2645 individuals, representing a mortality of approximately 97 % from the egg stage (Fig. 3). In autumn 2009, the number of age 1+ years and older fish in fresh water was estimated to be 636 individuals (Fig. 3), with apparently a very high mortality of 1+ fish in this year compared to previous years (data not shown) and most sampled being 2+ years. This was reflected in the smolt run the following spring, with an estimated 577 smolts passing through the trap, representing some 91 % of the estimated freshwater population of 1+ and older fish the previous autumn. This implies a very high rate of anadromy in this population. The egg-to-smolt survival rate was 0.65 % for this cohort.

Returns of VI marked adults in 2009 (43 spawners from 1170 smolts tagged in the preceding two years) indicated marine survival of around 3.5 %. Only about a third of spawners were marked (35 %), however, implying either a high straying rate, high tag loss or some combination of these. Presence of adipose fins on all unmarked fish suggests tag loss was not a factor. The 4 year (2007 – 2010) mean smolt production was 650 year^{-1} (range 457 - 857).

SMOLT AGES ACROSS CATCHMENTS

There was variation in the age structure of migrating smolts between the four catchments surveyed (Fig. 4), with no S4 smolts being detected in Mainland burns, and no S1 smolts being found in Hoy burns. There were also contrasts between burns on the same island, with Eyrland having a mean smolt age of 2 years, compared with 1 year in Bu. Similarly on Hoy, mean smolt age in Ore Burn was 2 years, contrasting with 3 years in Whaness. The proportion of S2 smolts was similar between Eyrland and Ore (both 83 %) and also between Bu and Whaness (both 38 %). The proportion of S3 smolts in each population was ranked in the order Whaness (58 %) > Ore (16 %) >Eyrland (6 %) > Bu (2 %).

ANALYSIS OF B-TYPE GROWTH

B-type growth was very common in smolts from Burn of Eyrland. All S1 smolts in both years exhibited B-type growth (Fig. 5), with declining proportions for S2 (95 % in 2007; 64 % in 2010) and S3 (83 % in 2007; 44 % in 2010) smolts. The differences between years suggests that freshwater growth was poorer in 2006 than in 2009, but unfortunately no detailed freshwater data were available for 2006 for comparison. Smolting *S. trutta* exhibited greater B-growth relative to same-aged non-smolting individuals. This difference was significant in 1 year old fish ($F_{1,261}$ = 14.589, $p < 0.001$) and two year olds ($F_{1,210}$ = 22.975, $p < 0.001$), whereas three year old smolts showed no significant difference ($F_{1,29} = 3.352$, $p > 0.05$). At both individual (Fig. 5) and population (Fig. 6) levels, there was a strong negative relationship between mean L_F at last annulus (L_{FcM}) and subsequent B-type growth of smolts in all three age classes across both years analysed, with the exception of individual S3 smolts in 2007 (Fig. 5). The relationships were stronger at the population level, as might be expected for pooled data, with a mean 83 % of variation in B-type growth being explained by L_{FcM} across all three age classes (Fig. 6). In contrast, analysis at the individual level showed more variability, with around 50 % and 30 % of variation in B-type growth attributable to L_{Fc} in S1 and S2 smolts, respectively, but a lower level of explanation for S3 smolts (Fig. 5). This arises from an increasing proportion of fish in older groups showing zero B-type growth (Fig. 5; also see above), which are smoothed out in the averaged data. There is also evidence of a minimum size for migration [as opposed to a threshold size for smolting, which could only apply the previous autumn at initiation of smolting; Økland *et al*. (1993)] of around 15 cm L_F. This is clear for S1smolts, but less so for S2 and S3 smolts. However, if only fish of L_{Fc} below 15cm are considered, the relationship between L_{Fc} and B-type growth is strengthened for S2 fish. For S3 smolts, most are already 15 cm L_F or more by the last annulus, so there are too few smaller fish to analyse, but in 2007 the few smaller S3 fish available also suggest this is true (Fig. 5). The strong negative relationships of B-type growth with L_{Fc} and L_{FcM} imply that this represents a compensatory growth response in smaller fish in freshwater immediately prior to migration in order to attain minimum migration size.

DISCUSSION

In the present study, near simultaneous surveys of four catchments were achieved by a single researcher with volunteer assistants over a sustained period. This provided a whole catchment population budget, as well as between catchment comparisons of factors affecting smolt age and B-type growth not previously available from larger systems. This supports the value of small catchment studies in providing a practicable approach to understanding key features of the anadromous *S. trutta* life-history. The utility of this study was enhanced by the habitat variation available around the semi-enclosed marine environment of Scapa Flow.

COHORT ANALYSIS FOR BURN OF EYRLAND

The Burn of Eyrland cohort study gives an overview of an anadromous S. *trutta* producing system not available so far in the published literature. To date, most studies on anadromous S. *trutta* have focused on smolt trapping (e.g. Byrne *et al*., 2004), with little information available on freshwater stages underpinning smolt production, except in the context of the contribution of migrant spawners to juvenile production (Charles *et al*., 2004). An exception to this was the extensive work of Elliot (see Elliot 1994 for review) on an upper catchment Lake District stream in the UK, where the focus was entirely on freshwater stages. However, this was only one tributary of a larger system, and overall smolt production of the whole system was not addressed. This highlights the logistic problems of working on large catchments, in terms of the trade-off between detailed data and logistics, and the advantages of small systems in answering key life history questions.

The estimate of marine survival from VI tagging returns, at only 3.5 %, was probably too low, given high numbers of untagged fish which must represent strays, since effectively the whole smolt run from Burn of Eyreland was tagged and adipose fin-clipped in both preceding years. This would imply a straying rate of around 65 % for 2009. Such a high straying rate of spawners, has not been previously reported for sea trout, although Berg & Berg (1987) found a 15 % straying rate in Norway. Nevertheless, confidence in this result is increased owing to the entire spawning also being effectively intercepted. The high rate of straying may be related to small catchment size and the nearby availability of other burns, consistent with the similar suggestion made for a collection of small streams on Gotland (Laikre *et al*., 2002). This raises interesting questions for further investigation regarding the genetic linkage between small systems and the potential for rescue effects in the event of local catastrophe in freshwater. Laikre et al. (2002) found limited genetic differentiation between sea rtout across 13 Gotland streams, and inferred straying as an important factor in maintaining small effective breeding populations, similar in size to those reported here (around 30 females, compared with about 50 here).

The present study of the Eyrland system also reveals the potential anadromous S. *trutta* production of a small stream system, with around 650 smolts produced each year. With an annual spawning run of around 100 spawners coming mainly from 1 sea winter (SW) and 2SW fish this implies a marine mortality of about 92 %, which is consistent with estimates from studies on salmon (Chaput, 2012). It is also in line with the estimate from VI tag returns (*c*. 96 %) estimated above, especially as the latter value is likely to be inflated as a result of some surviving marked fish straying to other burns and not being detected. To our knowledge, this is the first published estimate of sea trout marine mortality.

The estimated egg deposition from returning spawners in 2007 suggests that this is not limiting juvenile production in this system, the implication being that at present the system is sustainable, in spite of apparently high marine mortality . This will, however, be affected by any variation in egg-to-smolt survival, as noted by Chaput (2012) for salmon, which might be expected to be volatile in small systems in response to, for example, effects of climate change. The systems investigated here could provide key information on climate change effects such as alterations in river discharge patterns, which would be expected to be amplified in small streams (Isaak et al., 2012).

SMOLT AGES ACROSS CATCHMENTS

Variation in mean smolt age across such short geographical distances has not previously been reported. The marked variation in mean smolt age (from S1 to S3) across the four catchments surveyed, whose mouths are separated by only about 10 km, indicates clearly the effect of nutrient status on growth and subsequent smolt production independent of latitudinal effects of temperature, photoperiod or growing season. This effect is further emphasized by the possibility, noted above, that the systems may be linked by straying spawners, which would reduce effects of genetic selection. The observed variation in smolt age increases the complexity of the stock in the marine environment, and perhaps hedges against environmental fluctuations in different catchments, given the apparently high frequency of straying by spawners. This would suggest that these small catchments might require management on a metacatchment basis, as proposed by Laikre *et al.* (2002), rather than at a single river level, although genetic information would be required to underpin this. Whether this could also apply to larger catchments raises the key question of how connected such systems might be with respect to anadromous S. *trutta*, and whether a different management system might be needed for such populations compared to that traditionally applied to salmon, and by default also to the former.

ANALYSIS OF B-TYPE GROWTH

Despite the assertion of Went (1962) that B-type growth is a freshwater phenomenon, evidence of accelerated growth at the edge of scales associated with smolt migration (usually read from adult scales) have often been classed as "run out" growth, associated with passage through estuarine conditions (and by implication, increased food availability) on the way to sea (Poole, 2011). However, the current data show conclusively that B-type growth in anadromous S. *trutta* occurs in freshwater prior to migration, since the fish were trapped before sea entry, above an effectively impassable barrier (for parr or smolts). The further observation that the extent of B-type growth is negatively correlated with size at last annulus before migration implies strongly that it represents a compensatory response by smaller fish to gain size before migration. This is further supported by the observation that B-type growth is seen more frequently in smolts in the later part of the run. In other words, larger fish are ready to migrate earlier, whereas smaller fish stay longer in freshwater in order to gain size immediately prior to migration. That younger anadromous S. *trutta* smolts show more B-type growth was previously reported (Went 1949), but has seldom been looked at subsequently, as it has been stated that identification of "run-out" growth on scales from adult anadromous S. *trutta* is "usually too difficult" (Elliot

& Chambers 1996). The relationship of size, B-type growth and time of migration within the run has potential implications for sea survival, as it is often assumed that earlier migrants survive better than those later in the run (Bohlin *et al*., 1993) and that this correlates with size (Hoar, 1988; Dieperink *et al*. 2002; Saloniemi *et al*., 2004), earlier migrants being larger. Initial survival at sea should, therefore, be better in systems where older smolts predominate and B-type growth would be less important (from the results here), but could be compromised for smaller smolts from more productive systems where S1 or S2 smolts relying on B-type growth might predominate. This could have the paradoxical consequence that systems with good freshwater habitat and productivity might be at greatest risk from poor marine survival resulting from smaller mean smolt size.

The suggestion made here of an apparent minimum size for migration seems to be at odds with the assertion of Økland *et al*. (1993) that no threshold for smolting exists. However, Økland *et al*. (1993) address the possibility of a threshold in the previous autumn rather than a minimum size immediately before migration in spring. Furthermore, they estimate parr and smolt sizes by back calculation from adult scales, which may not account for B-type growth in smaller smolts and consequently may underestimate their size at smolting, but not that of larger smolts, so potentially confounding their analysis.

In conclusion, the study of small anadromous S. *trutta* systems in Orkney has provided clear answers to some key questions which were not directly tractable through studies of larger river systems. It has also indicated the potential for small catchments to contribute significantly to anadromous S. *trutta* populations and potentially to support their production in adjacent systems through high straying (spill-over) rates. It is suggested that intensive study of small systems is a cost-effective measure that should become a key element underpinning anadromous S. *trutta*, as distinct from Atlantic salmon, management into the future.

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Tables

Table I: Catchment details for the burns of Eyrland, Bu, Ore and Whaness. Length estimates include main tributaries only (estimated mean width > 0.75 m). Discharge = annual mean water flow. Catchment and discharge data supplied by the Scottish Environment Protection Agency. NGRs relate to burn mouths.

Burn	OS NGR[a]	Stream length, km	Mean altitude, m	Maximum altitude, m	Discharge, cumecs[b]	Catchment area, km^2
Eyrland	HY 293 095	10.01	65	144	0.176	8.132
Bu	HY 335 043	4.51	46	140	0.068	3.404
Ore	ND 305 938	7.01	42	111	0.138	7.956
Whaness	HY 244 027	7.2	56	241	0.068	5.279

[a] OS NGR – UK Ordnance Survey National Grid Reference
[b] cumecs – cubic metres per second

Table II: The four- stage scale used to categorise individual trout (*Salmo trutta*) as to their smolting status.

Category	Description	Counted in smolt analyses?
FW[a]	Markings typical of brown trout in freshwater, *i.e.* olive/brown with red and black spots, parr marks maybe visible, no silvering, scales not easily removed. Smolting not imminent.	No
M1[b]	Brown trout markings as above but showing some signs of silvering, scales easier to remove. Smolting possible but not certain.	No
M2	Fish silvering, red spots fading or gone, but black spots remain; scales easily removed. Smolting imminent.	Yes
M3	Fish almost entirely silver with few black spots, scales easily removed. Smolting imminent.	Yes

[a] FW = fresh water; [b] M = Migrant.

Figure Legends Thomson & Lyndon FSBI17

Fig 1: Map of Scapa Flow area of the Orkney Isles, UK. The sampled burns (streams) are indicated: Eyrland and Bu on Orkney Mainland; Whaness and Ore on island of Hoy. Scapa Flow is an enclosed marine environment, the eastern openings being separated from the North Sea by solid causeways (Churchill Barriers). Inset: location of Orkney Isles in United Kingdom.

Fig 2: Scale from a smolt sampled from Burn of Eyrland showing B-type growth at the outer edge (indicated by double arrow). There are two freshwater annuli (i.e. the smolt was S2).

Fig 3: Cohort analysis from egg to smolt for trout (*Salmo trutta*) in the Burn of Eyrland, 2007-2010. Egg numbers were estimated from Solomon (1997). Numbers of 0+ and older fish were estimated for whole catchment from electrofishing surveys in autumn of 2008 and 2009, respectively. Smolt numbers were derived from downstream trapping in 2010. 1++ = fish of 1+ and older (including residents).

Fig 4: Age structure of smolts (% of run in each catchment) captured during the smolt run by electrofishing or trapping from four catchments in Orkney, two on the Mainland (Eyrland and Bu) and two on Hoy (Ore and Whaness). Smolt ages are S1 (grey bars), S2 (hatched bars), S3 (open bars) and S4 (black bars). No S4 smolts were found in Mainland burns and no S1 smolts were found in Hoy burns.

Fig 5: Relationship between back-calculated FL at end of winter (cFL) and amount of B-type growth achieved by the time of sampling during the smolt run for individual S1, S2 and S3 smolts in 2007 (crosses; S1: $R^2 = 0.509$, $p < 0.001$, $n = 89$; S2, $R^2 = 0.378$, $p < 0.001$, $n = 332$; S3, $p > 0.1$ NS, $n = 24$) and 2010 (open circles; S1, $R^2 = 0.499$, $p < 0.001$,$n = 29$; S2, $R^2 = 0.292$, $p < 0.001$, $n = 81$; S3, $R^2 = 0.264$, $p < 0.001$, $n = 32$).

Fig 6: Relationship between back-calculated mean fork length (cMFL) at the end of the last winter before migration and the extent of B-type growth achieved subsequently in S1 (x; $R^2 = 0.859$, $p < 0.05$), S2 (o; $R^2 = 0.810$, $p < 0.05$) and S3 (+; $R^2 = 0.811$, $p < 0.05$) smolts sampled from the Burn of Eyrland, 2005 – 2010.

Fig. 1

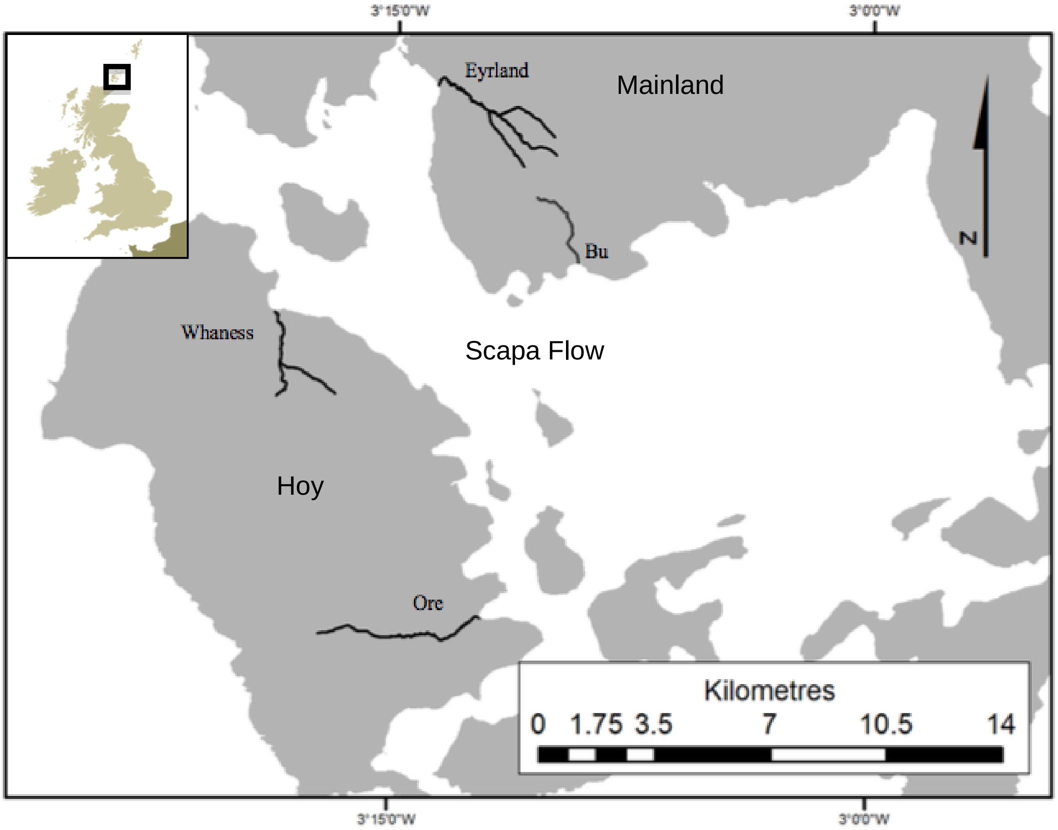

3°15'0"W
3°0'0"W
Eyrland
Mainland
Bu
N
Whaness
Scapa Flow
Hoy
Ore
Kilometres
0
1.75
3.5
7
10.5
14
3°15'0"W
3°0'0"W

Fig. 2

Fig. 3


Total population, log scale
100000
10000
1000
100
10
1
Eggs 2007
0+ 2008
1++2009
smolts 2010
Life stage and year

Fig. 4

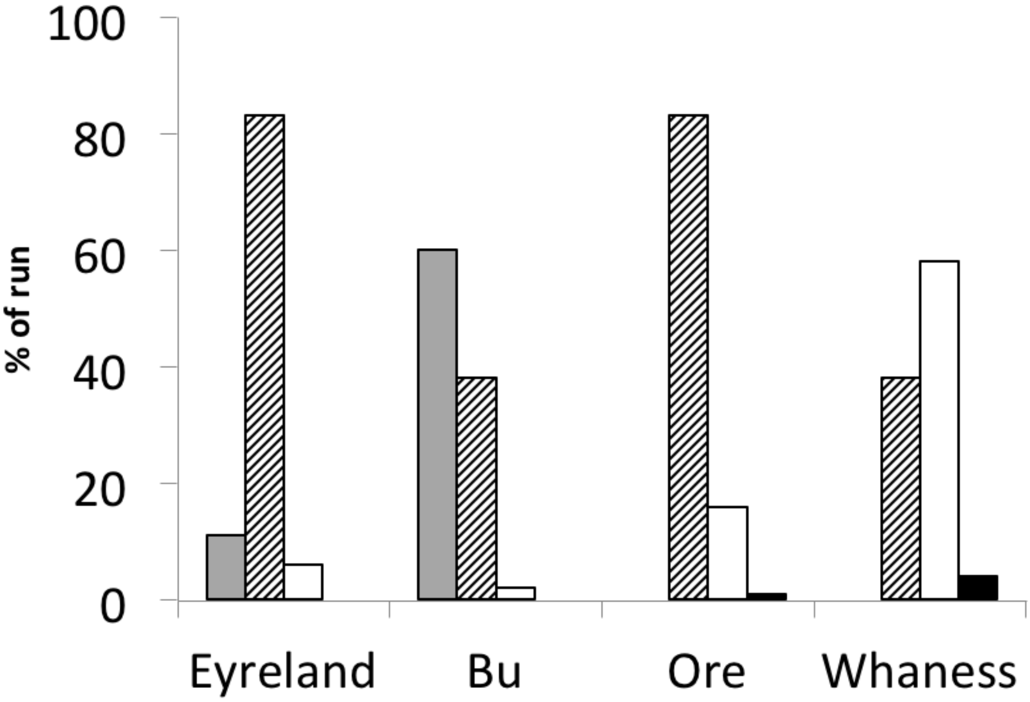


Fig. 5

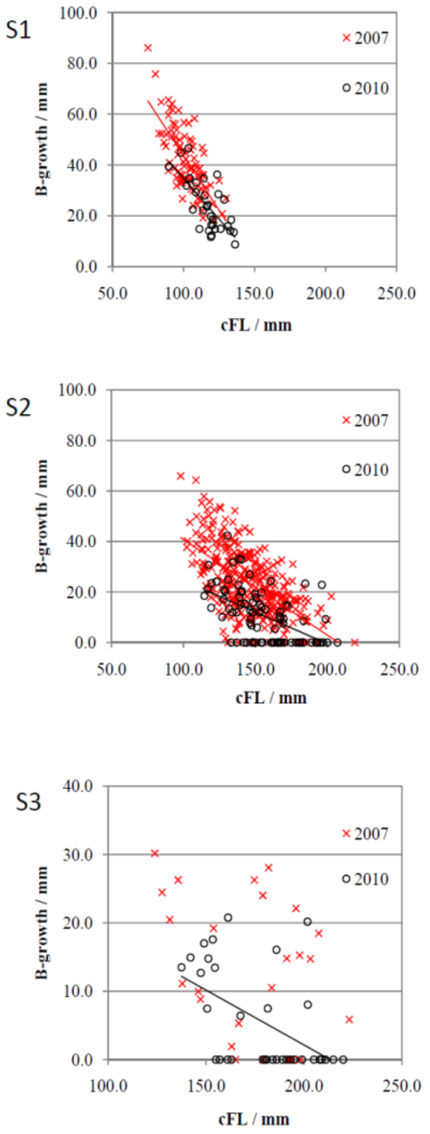
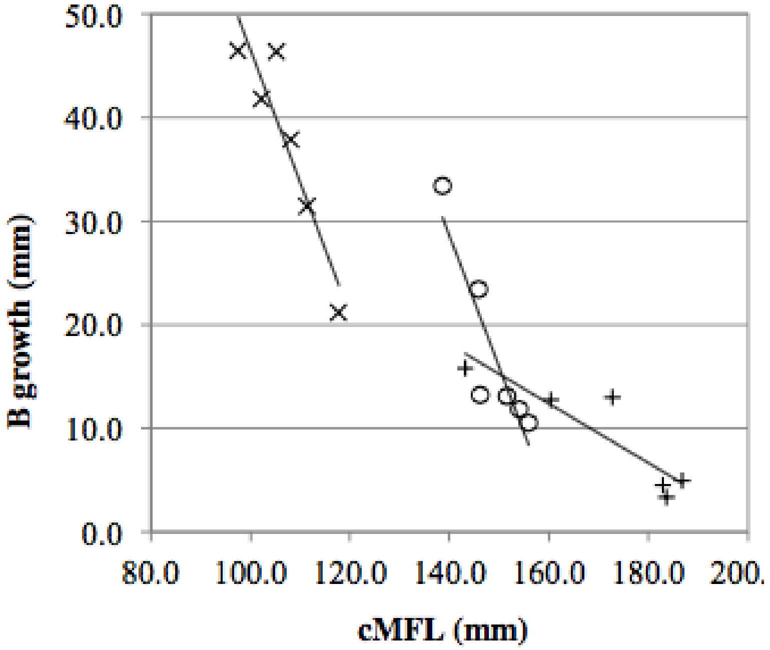

S1
B-growth / mm
100.0
80.0
60.0
40.0
20.0
0.0
50.0
100.0
150.0
200.0
250.0
cFL / mm
× 2007
○ 2010
S2
B-growth / mm
100.0
80.0
60.0
40.0
20.0
0.0
50.0
100.0
150.0
200.0
250.0
cFL / mm
× 2007
○ 2010
S3
B-growth / mm
40.0
30.0
20.0
10.0
0.0
100.0
150.0
200.0
250.0
cFL / mm
× 2007
○ 2010

Fig. 6


B growth (mm)
50.0
40.0
30.0
20.0
10.0
0.0
80.0
100.0
120.0
140.0
160.0
180.0
200.
cMFL (mm)