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Comparing anadromous brown trout *Salmo trutta* in small, neighbouring catchments across contrasting landscapes

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

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Running Head: Orkney *S. trutta* across landscapes

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Abstract

28 Study of anadromous brown trout in Orkney burns (small streams) with a common-
29 garden sea in Scapa Flow supports the key role of nutrient availability in fresh water,
30 independent of day length, as a determinant of smolt age, with a systematic increase
31 in mean smolt age from 1 to 3 years related inversely to productivity. Whole
32 catchment (8 km²) population budgets indicated annual smolt production of around
33 650 from approximately 100 spawners. Egg to smolt survival was 0.65 %, while
34 marine survival was estimated from mark recapture to be between 3.5 and 10 %. The
35 question of B-type growth (accelerated growth immediately prior to or during smolt
36 migration) was also addressed, with a strong negative correlation between B-type
37 growth and size at end of winter suggesting that this represents a freshwater
38 compensatory growth response,. The data obtained indicate the potential importance
39 of small catchments for supporting anadromous *Salmo trutta* populations and suggest
40 that small runs of spawners (< 100 individuals) are adequate to maintain stocks in
41 such situations. They also support the key role of freshwater productivity in
42 determining life-history characteristics over small spatial scales, with Orkney
43 providing a useful natural laboratory for future research into metapopulation genetic
44 structuring and environmental factors at a tractable scale.

45

46

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

49

50

INTRODUCTION

51

52

53

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

69

70 Little research is available on the biology of anadromous *S. trutta* in small
71 rivers (maximum channel width < 6 m) although *S. trutta* are more abundant *than S.*
72 *salar* in such rivers (Milner *et al.*, 2006b). Most previous studies of small streams
73 have focussed on either a single catchment (Mortensen, 1977; Rubin *et al.*, 2004;
74 Ayllon *et al.*, 2006) or relatively widely spaced streams (Jonsson *et al.* 2001). An
75 exception was the work of Laikre *et al.* (2002), that examined genetic relationships

76 across 13 streams on the Baltic island of Gotland, although ecological and life-history
77 variation across catchments were not considered.

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

88

89 Another question which has rarely been addressed in the anadromous *S. trutta*
90 literature is the phenomenon of so-called B-type growth [accelerated growth prior to
91 or during the smolt migration (Went, 1938, 1949; Fahy, 1990), also referred to as
92 spring (Heidarsson *et al.*, 2006) or run-out (Poole, 2011) growth] and in particular its
93 relationship with freshwater environmental conditions, smolt age and transition to
94 marine conditions. B-type smolts, which exhibit such growth, are contrasted against
95 A-type smolts, which migrate without any growth beyond the last annulus (Went,
96 1938; Thomson, 2015). An association of B-type growth with smolt age might help to
97 reconcile views on whether there is a threshold size for migration, [supported by Fahy
98 (1990), rejected by Økland *et al.* (2003)] and how this relates to other environmental
99 conditions.

100

101 The present paper addresses the themes selected above from Milner et al.
102 (2006a) through examination of anadromous *S. trutta* populations in the Orkney
103 Islands, off northern Scotland, U.K. The nature of Orkney’s environment, especially
104 around the enclosed marine basin of Scapa Flow (Fig 1), provides an excellent
105 situation for detailed study of anadromous *S. trutta* compared to larger systems
106 elsewhere. The small size of Orkney burns (streams) eases sampling of their trout
107 populations over short timescales, whilst it also means that *S. salar* are absent
108 (Thomson 2015), thus simplifying analyses. More importantly, the existence of
109 numerous anadromous *S. trutta* populations across contrasting habitats in a confined
110 region with a common-garden sea means that effects of latitude (Jonsson & L’Abée-
111 Lund, 1993; Jonsson *et al.*, 2001) and marine variation can be removed as influences,
112 facilitating clearer assessment of other parameters such as temperature, land-use and
113 stream size. Similarly, the complication of lacustrine features is removed in Orkney
114 burns, as most have none.

115

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

123

124

125

MATERIALS & METHODS

126

127

128 STUDY SITES

129 Previous work (Thomson 2015) identified catchments in Orkney supporting
130 populations of anadromous *S. trutta*. Four of these, which discharge into Scapa Flow,
131 were selected for more intensive study because of their contrasting characteristics
132 (Fig. 1 and Table I). Two catchments (Whaness and Ore Burns) were on the island of
133 Hoy, which is characterized by peatland and heather moorland (Land Use
134 Consultants, 1998), meaning that they are relatively oligotrophic. Ore Burn has a
135 simple single stem structure without major tributaries, but a relatively high discharge
136 (Table I). Whaness Burn has a single tributary, but lower discharge (Table I). The
137 other two catchments (Eyrland and Bu Burns) were on the Orkney Mainland. Burn of
138 Eyrland is the largest non-lacustrine catchment in Orkney (Table I). It rises on heather
139 moorland but then flows through improved grazing land over much of its length. Bu
140 Burn is short (Table I) and comprises a single stem with no significant tributaries,
141 flowing entirely through grazing land. Both Mainland burns rise at a similar altitude
142 (140 m) and are relatively eutrophic, Bu Burn more so than Eyrland (authors, pers.
143 obs.). Between the four catchments there are thus contrasts between structure, nutrient
144 status, altitude and discharge, but all have a common marine environment in Scapa
145 Flow.

146

147 ELECTROFISHING

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

151 0-400 V smoothed DC. Electrofishing protocols followed those of the Scottish
152 Fisheries Co-ordination Centre (SFCC, 2007). All surveys involved two people, one
153 using the electrofishing equipment, the other with a hand net and bucket to retain the
154 catch. After a brief test, to adjust the voltage, fishing was in an upstream direction, the
155 anode being moved side-to-side ensuring coverage across the entire burn width.
156 Voltage was 150 V, unless larger trout were expected, when lower settings were used.

157

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

162

163 TRAPPING

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

168

169 *Downstream trap*

170 The smolt (downstream) trap was installed each spring between 2007 and
171 2010 in the form of an inclined plane or “Wolf” trap (Wolf, 1951). This involved
172 blocking the fish ladder and channelling water over the dam and through a set of
173 screens extending 1.2 m from the dam lip and sloping (20°) downwards. The spacing
174 of the screen bars was 10 – 11 mm. An irrigated plastic trough, perpendicular to the

175 water flow along the bottom of the screens, led via a short pipe to a lidded holding
176 box.

177

178 *Upstream trap*

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

191

192 *Fish processing*

193 After capture, all fish were anaesthetized [2-phenoxyethanol (Sigma, UK), 0.5
194 ml/l] in small batches (parr and smolts) or individually (adults) to allow weighing
195 (Mettler Digital Battery Scale; www.mt.com), length measurement, scale sampling
196 and, for smolts only, visible implant (VI) tagging (Northwest Marine Technology
197 Ltd.; www.nmt.us), adipose fin-clipping of all VI tagged fish and classification of
198 smolting status (Table II). Fish were placed in a bucket of clean water where they

199 recovered within 2 min. They were then carefully released back into the water-
200 course. Scale samples were retained in individually labelled paper packets for later
201 reading.

202

203 *Downstream Trap Efficiency*

204 A sub-sample of smolts was tagged and released upstream of the trap.
205 Efficiency was calculated as the percentage of marked smolts recaptured as they
206 repeated their downstream movement through the trap, including any which were
207 captured the following year. The mean trap efficiency calculated across 2008 and
208 2009 was 72.8 %.

209

210 COHORT ANALYSIS FOR BURN OF EYRLAND

211 Scale reading was done using a Zeiss Axiostar compound microscope (40x
212 magnification; www.zeiss.com) with a mounted digital camera (9 MP resolution) to
213 record images of all scales. Scale reading and fish-size back-calculation followed the
214 method of Elliott & Chambers (1996). Estimation of egg deposition was based on
215 fecundity data for anadromous *S. trutta* (Solomon 1997), along with median length
216 and number of returning females recorded in 2007. Such individuals were
217 distinguished from males by their lack of facial remodeling (kype formation) and lack
218 of milt expression. The short length and small size of this burn meant that
219 anadromous *S. trutta* entering from the sea were on the point of spawning, so that
220 these characteristics were considered an accurate indicator of sex ratio. Numbers of
221 0+ year fish were determined the autumn after spawners had returned (2008) by
222 electrofishing survey at 9 sites. Area fished, stream length and median width were

223 combined to give a total population estimate. Numbers of age 1+ years and older fish
224 were similarly surveyed in autumn 2009, and smolt production estimated from
225 downstream trapping in the spring of 2010 corrected by application of the mean trap
226 efficiency.

227

228 SMOLT AGES ACROSS CATCHMENTS

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

233

234 ANALYSIS OF B-TYPE GROWTH

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

245

246 STATISTICAL ANALYSES

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

253

254

RESULTS

255

COHORT ANALYSIS FOR BURN OF EYRLAND

257 The median size of returning female anadromous *S. trutta* ($n = 51$) in autumn
258 2007 was 45 cm. Using Soloman's (1997) mean line for British anadromous *S. trutta*
259 fecundity gave an estimated egg abundance of 88 170 (Fig. 3). The following autumn
260 (2008), the population of 0+ year *S. trutta* in Burn of Eyrland catchment was
261 estimated to be 2645 individuals, representing a mortality of approximately 97 %
262 from the egg stage (Fig. 3). In autumn 2009, the number of age 1+ years and older
263 fish in fresh water was estimated to be 636 individuals (Fig. 3), with apparently a very
264 high mortality of 1+ fish in this year compared to previous years (data not shown) and
265 most sampled being 2+ years. This was reflected in the smolt run the following
266 spring, with an estimated 577 smolts passing through the trap, representing some 91
267 % of the estimated freshwater population of 1+ and older fish the previous autumn.
268 This implies a very high rate of anadromy in this population. The egg-to-smolt
269 survival rate was 0.65 % for this cohort.

270 Returns of VI marked adults in 2009 (43 spawners from 1170 smolts tagged in
271 the preceding two years) indicated marine survival of around 3.5 %. Only about a

272 third of spawners were marked (35 %), however, implying either a high straying rate,
273 high tag loss or some combination of these. Presence of adipose fins on all unmarked
274 fish suggests tag loss was not a factor. The 4 year (2007 – 2010) mean smolt
275 production was 650 year⁻¹ (range 457 - 857).

276

277 SMOLT AGES ACROSS CATCHMENTS

278 There was variation in the age structure of migrating smolts between the four
279 catchments surveyed (Fig. 4), with no S4 smolts being detected in Mainland burns,
280 and no S1 smolts being found in Hoy burns. There were also contrasts between burns
281 on the same island, with Eyrland having a mean smolt age of 2 years, compared with
282 1 year in Bu. Similarly on Hoy, mean smolt age in Ore Burn was 2 years, contrasting
283 with 3 years in Whaness. The proportion of S2 smolts was similar between Eyrland
284 and Ore (both 83 %) and also between Bu and Whaness (both 38 %). The proportion
285 of S3 smolts in each population was ranked in the order Whaness (58 %) > Ore (16
286 %) > Eyrland (6 %) > Bu (2 %).

287

288 ANALYSIS OF B-TYPE GROWTH

289 B-type growth was very common in smolts from Burn of Eyrland. All S1
290 smolts in both years exhibited B-type growth (Fig. 5), with declining proportions for
291 S2 (95 % in 2007; 64 % in 2010) and S3 (83 % in 2007; 44 % in 2010) smolts. The
292 differences between years suggests that freshwater growth was poorer in 2006 than in
293 2009, but unfortunately no detailed freshwater data were available for 2006 for
294 comparison. Smolting *S. trutta* exhibited greater B-growth relative to same-aged non-
295 smolting individuals. This difference was significant in 1 year old fish ($F_{1,261} =$
296 14.589, $p < 0.001$) and two year olds ($F_{1,210} = 22.975$, $p < 0.001$), whereas three year

297 old smolts showed no significant difference ($F_{1,29} = 3.352, p > 0.05$). At both
298 individual (Fig. 5) and population (Fig. 6) levels, there was a strong negative
299 relationship between mean L_F at last annulus (L_{FcM}) and subsequent B-type growth of
300 smolts in all three age classes across both years analysed, with the exception of
301 individual S3 smolts in 2007 (Fig. 5). The relationships were stronger at the
302 population level, as might be expected for pooled data, with a mean 83 % of variation
303 in B-type growth being explained by L_{FcM} across all three age classes (Fig. 6). In
304 contrast, analysis at the individual level showed more variability, with around 50 %
305 and 30 % of variation in B-type growth attributable to L_{Fc} in S1 and S2 smolts,
306 respectively, but a lower level of explanation for S3 smolts (Fig. 5). This arises from
307 an increasing proportion of fish in older groups showing zero B-type growth (Fig. 5;
308 also see above), which are smoothed out in the averaged data. There is also evidence
309 of a minimum size for migration [as opposed to a threshold size for smolting, which
310 could only apply the previous autumn at initiation of smolting; Økland *et al.* (1993)]
311 of around 15 cm L_F . This is clear for S1 smolts, but less so for S2 and S3 smolts.
312 However, if only fish of L_{Fc} below 15cm are considered, the relationship between L_{Fc}
313 and B-type growth is strengthened for S2 fish. For S3 smolts, most are already 15 cm
314 L_F or more by the last annulus, so there are too few smaller fish to analyse, but in
315 2007 the few smaller S3 fish available also suggest this is true (Fig. 5). The strong
316 negative relationships of B-type growth with L_{Fc} and L_{FcM} imply that this represents a
317 compensatory growth response in smaller fish in freshwater immediately prior to
318 migration in order to attain minimum migration size.

319
320
321

322

DISCUSSION

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

331

COHORT ANALYSIS FOR BURN OF EYRLAND

333 The Burn of Eyrland cohort study gives an overview of an anadromous *S.*
334 *trutta* producing system not available so far in the published literature. To date, most
335 studies on anadromous *S. trutta* have focused on smolt trapping (e.g. Byrne *et al.*,
336 2004), with little information available on freshwater stages underpinning smolt
337 production, except in the context of the contribution of migrant spawners to juvenile
338 production (Charles *et al.*, 2004). An exception to this was the extensive work of
339 Elliot (see Elliot 1994 for review) on an upper catchment Lake District stream in the
340 UK, where the focus was entirely on freshwater stages. However, this was only one
341 tributary of a larger system, and overall smolt production of the whole system was not
342 addressed. This highlights the logistic problems of working on large catchments, in
343 terms of the trade-off between detailed data and logistics, and the advantages of small
344 systems in answering key life history questions.

345

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

362

363 The present study of the Eyreland system also reveals the potential anadromous
364 *S. trutta* production of a small stream system, with around 650 smolts produced each
365 year. With an annual spawning run of around 100 spawners coming mainly from 1
366 sea winter (SW) and 2SW fish this implies a marine mortality of about 92 %, which is
367 consistent with estimates from studies on salmon (Chaput, 2012). It is also in line
368 with the estimate from VI tag returns (*c.* 96 %) estimated above, especially as the
369 latter value is likely to be inflated as a result of some surviving marked fish straying

370 to other burns and not being detected. To our knowledge, this is the first published
371 estimate of sea trout marine mortality.

372

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

382

383 SMOLT AGES ACROSS CATCHMENTS

384 Variation in mean smolt age across such short geographical distances has not
385 previously been reported. The marked variation in mean smolt age (from S1 to S3)
386 across the four catchments surveyed, whose mouths are separated by only about 10
387 km, indicates clearly the effect of nutrient status on growth and subsequent smolt
388 production independent of latitudinal effects of temperature, photoperiod or growing
389 season. This effect is further emphasized by the possibility, noted above, that the
390 systems may be linked by straying spawners, which would reduce effects of genetic
391 selection. The observed variation in smolt age increases the complexity of the stock
392 in the marine environment, and perhaps hedges against environmental fluctuations in
393 different catchments, given the apparently high frequency of straying by spawners.
394 This would suggest that these small catchments might require management on a meta-

395 catchment basis, as proposed by Laikre *et al.* (2002), rather than at a single river level,
396 although genetic information would be required to underpin this. Whether this could
397 also apply to larger catchments raises the key question of how connected such
398 systems might be with respect to anadromous *S. trutta*, and whether a different
399 management system might be needed for such populations compared to that
400 traditionally applied to salmon, and by default also to the former.

401

402 ANALYSIS OF B-TYPE GROWTH

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

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

431

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

440

441 In conclusion, the study of small anadromous *S. trutta* systems in Orkney has
442 provided clear answers to some key questions which were not directly tractable
443 through studies of larger river systems. It has also indicated the potential for small
444 catchments to contribute significantly to anadromous *S. trutta* populations and

445 potentially to support their production in adjacent systems through high straying
446 (spill-over) rates. It is suggested that intensive study of small systems is a cost-
447 effective measure that should become a key element underpinning anadromous S.
448 *trutta*, as distinct from Atlantic salmon, management into the future.

449

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462

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560 Tables

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562 **Table I:** Catchment details for the burns of Eyrland, Bu, Ore and Whaness. Length
563 estimates include main tributaries only (estimated mean width > 0.75 m). Discharge
564 = annual mean water flow. Catchment and discharge data supplied by the Scottish
565 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

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567 ^aOS NGR – UK Ordnance Survey National Grid Reference

568 ^bcumecs – cubic metres per second

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

575

Category	Description	Counted in smolt analyses?
FW ^a	Markings typical of brown trout in freshwater, <i>i.e.</i> 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

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577 ^aFW = fresh water; ^bM = Migrant.

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582 Figure Legends Thomson & Lyndon FSBI17

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

590

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

594

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

600

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

606

607 **Fig 5:** Relationship between back-calculated FL at end of winter (cFL) and amount of
608 B-type growth achieved by the time of sampling during the smolt run for individual
609 S1, S2 and S3 smolts in 2007 (crosses; S1: $R^2 = 0.509$, $p < 0.001$, $n = 89$; S2, $R^2 =$
610 0.378 , $p < 0.001$, $n = 332$; S3, $p > 0.1$ NS, $n = 24$) and 2010 (open circles; S1, $R^2 =$
611 0.499 , $p < 0.001$, $n = 29$; S2, $R^2 = 0.292$, $p < 0.001$, $n = 81$; S3, $R^2 = 0.264$, $p < 0.001$,
612 $n = 32$).

613 **Fig 6:** Relationship between back-calculated mean fork length (cMFL) at the end of
614 the last winter before migration and the extent of B-type growth achieved
615 subsequently in S1 (x; $R^2 = 0.859$, $p < 0.05$), S2 (o; $R^2 = 0.810$, $p < 0.05$) and S3 (+;
616 $R^2 = 0.811$, $p < 0.05$) smolts sampled from the Burn of Eyrland, 2005 – 2010.

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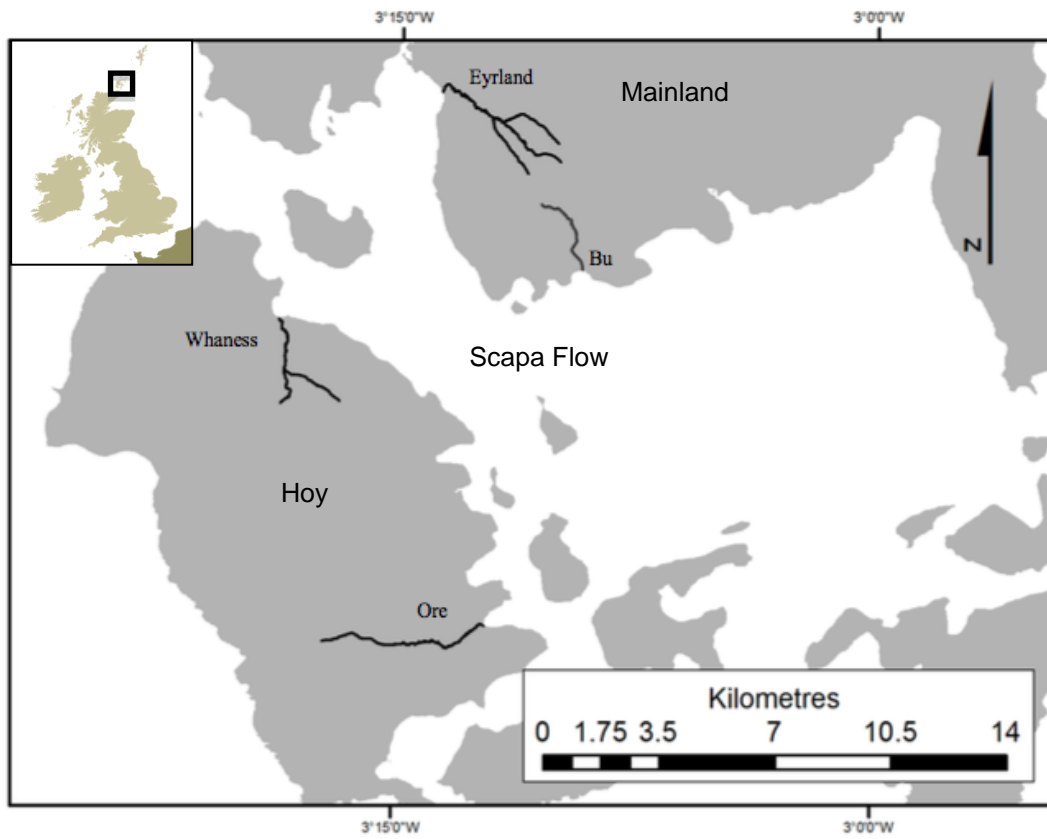
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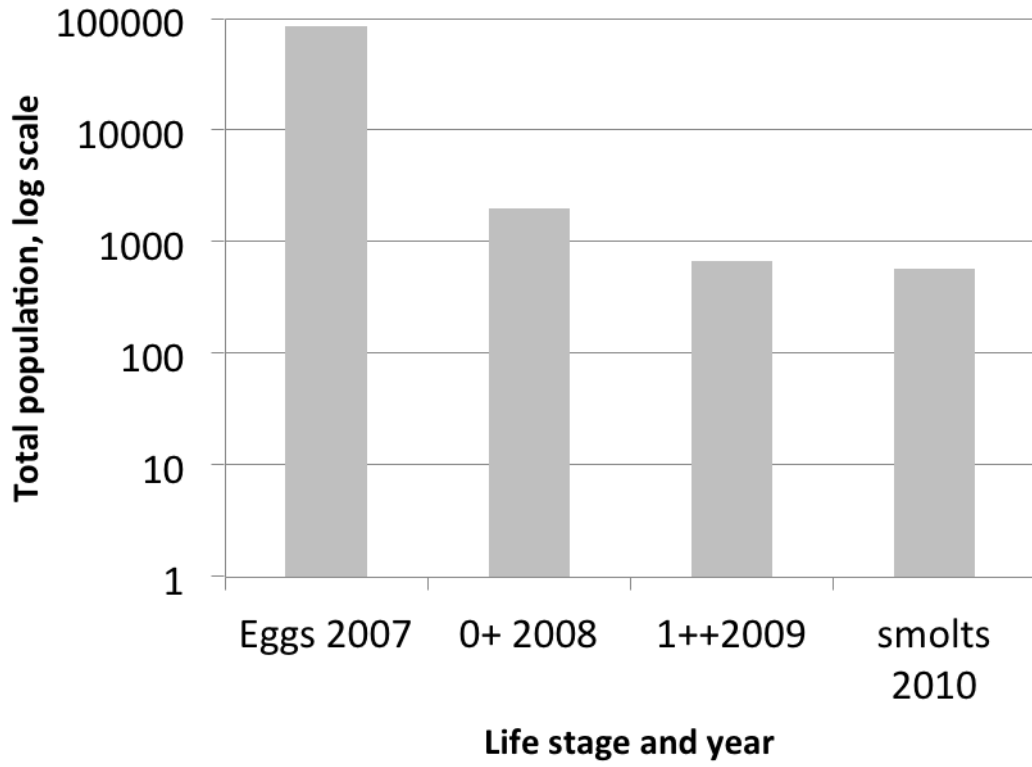
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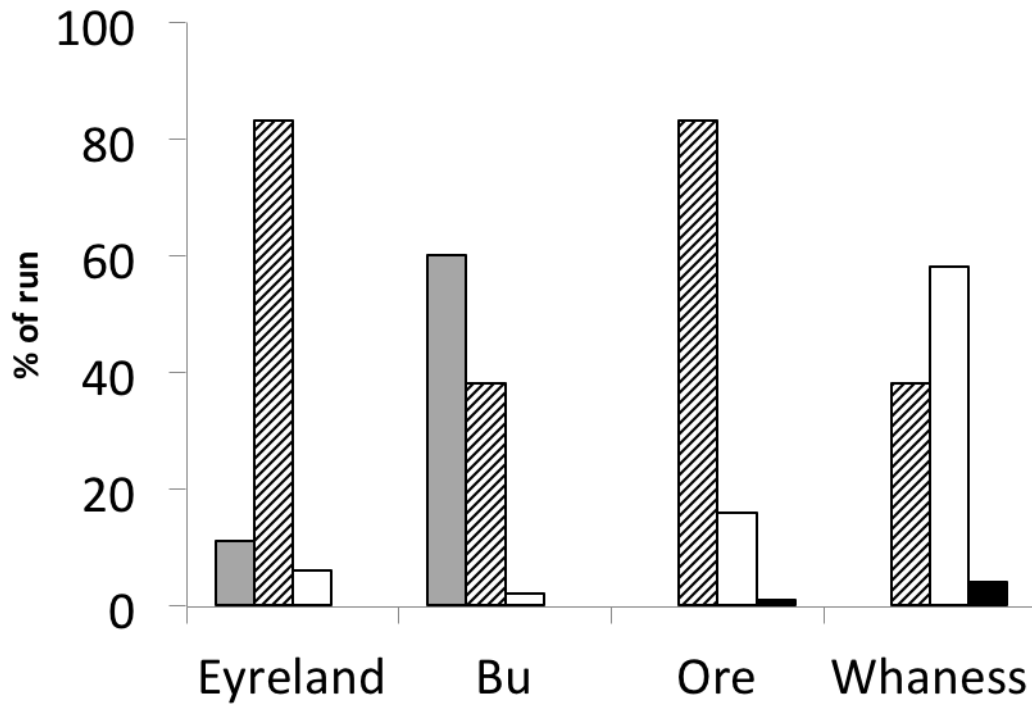
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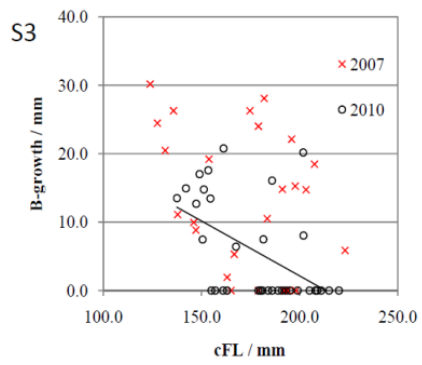
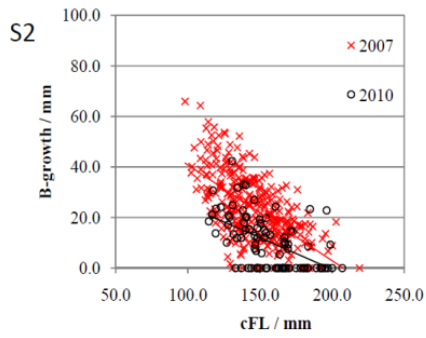
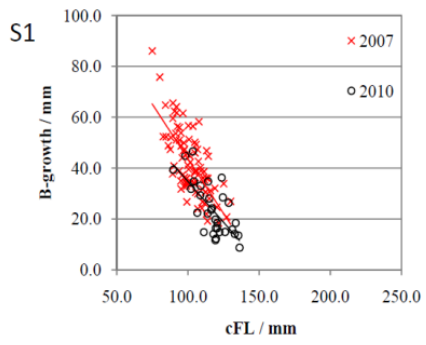
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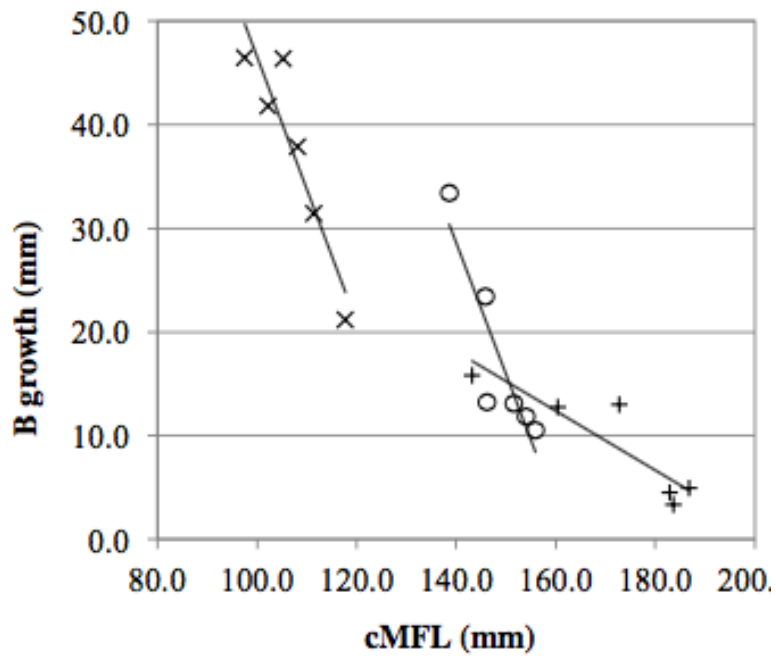
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738 Fig. 5
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757 Fig. 6
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