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**The response of North Atlantic diadromous fish to multiple stressors including land use change: a multidecadal study**

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1 **The response of North Atlantic diadromous fish to multiple stressors including land use**  
2 **change: a multidecadal study**

3

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23

24

25 **Abstract**

26 Reduction of freshwater habitat quality due to land use change can have significant impacts  
27 on diadromous fish. Partitioning this impact from other potential drivers, such as changing  
28 marine conditions and climate, is hampered by a lack of long term datasets. Here, four  
29 decades of data were used to assess the impact of land use change on *Salmo salar* L. and  
30 anadromous *Salmo trutta* L. in the Burrishoole catchment, Ireland, one of the few index sites  
31 for diadromous fish in the North Atlantic. Land use change was found to have no significant  
32 impact on the freshwater survival of either salmon or trout. However, climate impacted  
33 significantly on the survival of salmon and trout in freshwater, with poor survival in years  
34 with wetter warmer winters, coinciding with positive North Atlantic Oscillation values.  
35 Additionally, cold springs were associated with higher survival in trout. The addition of  
36 hatchery fish into the salmon spawning cohort coincided with low freshwater survival. Our  
37 results highlight the necessity for a broad ecosystem approach in any conservation effort of  
38 these species.

39

40

## 41 **Introduction**

42 The migratory nature of diadromous fish means that they are threatened by a unique set of  
43 multiple stressors, including habitat destruction, barriers, overexploitation and climate change  
44 (Wilcove and Wikelski 2008, Piou and Prévost 2013). As a result, declines have been  
45 catalogued around the globe (Musick et al. 2000, Limburg and Waldman 2009). Effective  
46 conservation of migratory fish requires an assessment of the relative importance of potential  
47 pressures, enabling managers to prioritise cost efficient programmes of measures aimed at  
48 priority impacts. It also requires an understanding and quantification of fundamental density  
49 dependant processes (Rose et al. 2001) and long term directional changes in stock recruitment  
50 relationships (non-stationarity) (Chaput et al. 2005, Walters et al. 2008).

51 In the north Atlantic region, declines in stocks of Atlantic salmon (*Salmo salar* L.)  
52 and anadromous brown trout (sea trout) (*Salmo trutta* L.) have been noted in recent years  
53 (Gargan et al. 2006, ICES 2014). A downward trend in salmon stock recruitment (returns of  
54 adults back to freshwater) has been evident from the mid-1980s across their Atlantic range  
55 (Crozier et al. 2003, Jonsson and Jonsson 2009). Sea trout populations along the west coast of  
56 Ireland declined in the late 1980s and early 1990s, a phenomenon that was linked to intensive  
57 salmon aquaculture in enclosed bays, resulting in high levels of sea lice *Lepeophtheirus*  
58 *salmonis* (Krøyer, 1837) and infestation of returning sea trout (Tully and Whelan 1993,  
59 Gargan et al. 2006, Poole et al. 2006). While some sea trout populations have recovered,  
60 many other populations remain at historically low levels (Gargan et al. 2006, Marine Institute  
61 2013). Marine mortality has been pinpointed as being the most significant driver of these  
62 species declines (Piou and Prévost 2013), however, impacts originating on land, including  
63 freshwater habitat loss, are regarded as easier to address (Bacon et al. 2015).

64 Declines in diadromous fish populations in their freshwater phases have been  
65 attributed to land use and management policies associated with afforestation, agriculture and

66 rural development (Elliott et al. 1998, Hendry et al. 2003). Habitat degradation has been  
67 identified as one of the biggest threats to freshwater vertebrates, particularly those aquatic  
68 species inhabiting flowing waters (Dudgeon et al. 2006, Stendera et al. 2012, Collen et al.  
69 2014). While a cause-effect relationship between land use change and fish stock decline is  
70 plausible and highly likely, questions remain about the relative contribution of this driver,  
71 and few accurate quantitative links have been established. Long-term datasets quantifying  
72 environmental change and the response of diadromous fish populations in the same  
73 catchment are extremely rare. Accurate quantification of diadromous fish migration into and  
74 out of catchments is difficult, and restricted to only a small number of index sites where full  
75 trapping facilities are available. For example, there are only 13 index stations collecting long  
76 term data on the stock and recruitment of Atlantic salmon in the NE Atlantic region (Prévost  
77 et al. 2003).

78 Atlantic salmon and anadromous brown trout are native to the Burrishoole catchment  
79 in the west of Ireland. At these latitudes, Atlantic salmon and anadromous trout spawn in  
80 winter and spend 1-4 years in freshwater before entering the sea as smolts (Metcalf and  
81 Thorpe 1990). They return to their natal rivers to spawn after one or more years. A long-term  
82 monitoring programme of migrating salmon and trout has enabled quantification of key  
83 trends in the Burrishoole diadromous fish populations from the 1960s to the present. In  
84 addition to the long-term fish population records, a detailed reconstruction of aquatic  
85 ecosystem responses to land use change in the Burrishoole in the 20<sup>th</sup> century is available  
86 (Dalton et al. 2014). This palaeolimnological reconstruction was described from a sediment  
87 core taken from the deepest point of Lough Feeagh, the most downstream lake in the  
88 Burrishoole catchment. Slices of this core were dated and analysed for commonly used  
89 palaeolimnological proxies, which enabled the key land use changes in the catchment to be  
90 quantified and dated. Low nutrient levels prevailed in the lakes in the catchment lakes until

91 the 1950s. Commercial coniferous afforestation in the mid-20<sup>th</sup> century and extensive sheep  
92 overgrazing in the 1980s and 1990s (Gillmor and Walsh 1993) were associated with  
93 increased rates of erosion, leading to elevated sedimentation, organic matter and nutrients in  
94 downstream lakes, and a shift to mesotrophic conditions (Dalton et al. 2014). This  
95 reconstruction provided valuable information that captured the degradation of the lake and its  
96 water catchment along a trajectory spanning the last century that is representative of many  
97 upland peat catchments on the Atlantic coast of Ireland (Huang and O'Connell 2000, Bullock  
98 et al. 2012) and beyond (Evans et al. 2014). In these catchments, afforestation and  
99 overgrazing have been a focus of fisheries and aquatic ecosystems conservation efforts  
100 (Fitzsimons and Igoe 2004, Drinan et al. 2013, Harrison et al. 2014).

101         These land use changes in the Burrishoole catchment could conceivably have  
102 impacted native diadromous fish populations. Higher levels of sediment in rivers may  
103 suffocate spawning beds, reducing egg survival of salmon and trout (Cowx et al. 1998,  
104 Soulsby et al. 2001, Suttle et al. 2004), while increases in trophic state can effect juvenile  
105 salmonid survival (Hendry et al. 2003). Recent work in Ireland has shown the deleterious  
106 effects of coniferous plantations on salmon populations, with upland streams in forested  
107 catchments having fewer salmon than those draining non-forested catchments (Harrison et al.  
108 2014). Trout were unaffected in that study, implying that there may be inter-specific  
109 differences in sensitivity to the changes in habitat quality associated with commercial conifer  
110 production.

111         Although focussed on the Burrishoole catchment, the co-availability of both fish  
112 census and environmental change data provides a unique opportunity to explore the role of  
113 changes in land use and freshwater habitat on important stocks of diadromous taxa,  
114 contributing to an issue that is of general concern: the long term conservation of fish stocks in  
115 a rapidly changing world.

116

117 **Materials and Methods**118 *Site description*

119 Burrishoole is a small (100 km<sup>2</sup>) upland catchment (53° 56' N, 9° 35' W) draining into the  
120 North-east Atlantic through Clew Bay (Fig. 1). Climatically influenced by the Atlantic Ocean  
121 (Jennings et al. 2000, Allott et al. 2005, Blenckner et al. 2007), the catchment experiences a  
122 temperate, oceanic climate with mild winters and relatively cool summers. Maximum  
123 summer air temperatures rarely exceed 20°C, while minimum winter temperatures are usually  
124 between 2°C and 4°C. The base geology on the western side of the catchment is  
125 predominantly quartzite and schist, leading to acidic runoff, with poor buffering capacity. By  
126 comparison, the geology on the eastern side is more complex as quartzite and schist are  
127 interspersed with veins of volcanic rock, dolomite and wacke, leading to higher buffering  
128 capacity and aquatic production. Soils in the catchment comprise poorly drained gleys, peaty  
129 podsoles and blanket peats. Feeagh and Bunaveela, the two largest freshwater lakes in the  
130 catchment, are both relatively deep (mean depth >12 m), oligotrophic (TP <10 ug l<sup>-1</sup>),  
131 coloured (c. 80 mg l<sup>-1</sup> PtCo) due to high levels of dissolved organic carbon (DOC), have low  
132 alkalinity (<20 mg l<sup>-1</sup> CaCO<sub>3</sub>) and are slightly acidic (pH = c. 6.7).

133 Partial upstream and downstream fish trapping facilities have been in operation in  
134 Burrishoole since 1958, and full trapping facilities were put in place in 1970. The traps  
135 enable a complete census of migrating fish in (adult salmon and sea trout) and out (salmon  
136 and trout smolts) of the catchment. A variable number of individuals from a captive bred  
137 population of salmon ('Burrishoole hatchery fish') were released upstream of the traps during  
138 the study period, and spawned along with the wild population. Census details are recorded in  
139 the annual reports of the research station (e.g. Marine Institute 2013). A rod fishery for  
140 salmon and trout operated during the time period of interest, between June and September of



141 each year. The salmon and sea trout catches have changed considerably since the 1970s. For  
142 example, the average number of salmon and sea trout caught in the period 1970-74 (including  
143 wild and hatchery fish) was 237 and 967 respectively. In 1996, the salmon catch was 295 but  
144 the sea trout catch had dropped to 125. Since 1995, all wild salmon fishing has been on a  
145 catch and release basis, with restrictions on fishing on Feeagh imposed for conservation  
146 reasons. Data from these fisheries are included in the census data where relevant (e.g. fish  
147 which were caught and released are including in the spawning escapement, while fish killed  
148 are not).

149

#### 150 *Data collation*

151 Data were collated to provide two fish response variables along with a suite of explanatory  
152 variables characterising land use change, climatic influences and other significant impacts  
153 (Fig. 2). The cut off year for data collation (2007) was chosen as it represents the most recent  
154 year of the catchment change reconstruction provided by the palaeolimnological record  
155 extracted from Lough Feeagh (Dalton et al. 2014). The fish response variables were salmon  
156 and trout freshwater survival (Fig. 2). The number of returning adult salmon and trout were  
157 counted as they moved upstream through the Burrishoole traps between 1970 and 2006. Egg  
158 number (the potential egg deposition of each cohort) was estimated using known sex ratios  
159 and fecundities. Sex ratios are estimated from external characteristics as they move upstream  
160 through the traps and are catalogued in the annual reports of the research station (e.g. Marine  
161 Institute 2013). As salmon fecundity (egg number per fish) can be predicted from fish size  
162 (de Eyto et al. 2015), fecundities are estimated from length: egg number relationships  
163 parameterised for Burrishoole fish, using egg numbers and fish size (length or weight)  
164 collected from brood stock (Marine Institute, unpublished data). In Burrishoole, the majority  
165 of salmon smolts migrate as two year old fish (2+), while trout generally smolt as 2+ and 3+

166 fish. Out-migrating smolts were counted as they moved down through the traps from 1973.  
167 Egg numbers were matched with the relevant smolt year for both salmon and trout, enabling  
168 the modelling of stock recruitment curves for each species (Fig. 3). In the case of trout, the  
169 smolt output was portioned between the potential proportion of 2+ and 3 + smolts (Poole et  
170 al. 2006). The residuals from these stock recruitment (SR) curves were used as the survival  
171 index for each species (Peterman et al. 1998, Mueter et al. 2002), with negative residuals  
172 indicating cohorts with lower than expected survival, and positive residuals indicting good  
173 survival. This survival index represents the survival of salmon and trout in the freshwater  
174 phase of their life cycle. If land use change is affecting the freshwater stages of salmonids at a  
175 catchment scale, then this is where the impacts are most likely to be seen. The number of  
176 hatchery salmon released upstream to spawn was included in the egg deposition estimate. The  
177 contribution of resident brown trout to the egg numbers was not quantified, and so the  
178 number of trout smolts migrating out is based on the assumption that they are the progeny of  
179 migrating trout. This is unlikely to be completely the case, and it is probable that a small,  
180 variable proportion of trout smolts derive from resident brown trout.

181 Land use change explanatory variables (n=14) were extracted from the analysis  
182 described in Dalton et al. (2014). As many of these explanatory variables were highly  
183 collinear, initial data exploration was used to extract a land use change proxy which  
184 adequately reflected the timing and direction of impacts on the downstream aquatic  
185 ecosystem (Lough Feeagh) (Fig. 2). Percentage loss on ignition (*LOI*) was measured at 1cm  
186 intervals from the Lough Feeagh core (Dalton et al. 2014). *LOI* quantifies changes in the  
187 proportion of organic material in sediment accumulating in the lake (Heiri et al. 2001). In an  
188 oligotrophic lake in a catchment that is largely blanketed in peat, major changes in the  
189 proportion of organic material in sediments are likely to represent variations in external  
190 loadings to the lake, as a result of peat erosion and inwash. *LOI* can therefore be used as a

191 proxy of catchment instability. The proportion of organic matter increased from baseline  
192 conditions of ~ 27% before 1960, and rose to 46% by the mid-1990s. It then decreased to  
193 ~40% after 2000. Twenty-six samples from the Lough Feeagh core were analysed for *LOI* in  
194 the time period for which salmonid data were available (1971-2007) and were matched to the  
195 relevant hatch year using a Constant Rate of Supply (CRS) model for determining  
196 accumulation rates (Appleby 2002). CRS estimates were validated with reference to <sup>137</sup>Cs  
197 fallout chronostratigraphic markers (1986 Chernobyl and 1963 weapons testing).

198         While the aim of this paper was to estimate the role that land use change has played in  
199 the population dynamics of fish in Burrishoole, previous research has highlighted several  
200 climatic and other factors (Fig. 2) accounting for some of the observed variation in  
201 Burrishoole salmon and trout trends (McGinnity et al. 2009). Water temperature was  
202 measured adjacent to the fish trap on the eastern outflow from Lough Feeagh (Fig. 1) using a  
203 paper chart recorder. Data were extracted at midnight for each day, and averaged to produce  
204 seasonal values (winter – Dec, Jan, Feb; spring – Mar, Apr, May; summer – Jun, Jul, Aug;  
205 autumn – Sep, Oct, Nov) (Fig. 2). Similarly, precipitation measured at the Burrishoole  
206 manual weather station (Fig. 1) was expressed as seasonal accumulations of daily rainfall  
207 (Fig. 2). Both Dalton et al. (2014) and Jennings et al. (2000) highlighted the correlation  
208 between the NAO index and catchment responses in the Burrishoole, and so this index was  
209 included as a potential climatic explanatory variable (average values for the months of  
210 December, January, February, and March: Hurrells winter Index (Hurrell 1995) (Fig. 2).  
211 Previous analysis of the freshwater survival of salmon in Burrishoole has shown that the  
212 proportion of hatchery fish in the spawning cohort (which varied between 1 and 60% over the  
213 time series), accounted for a large proportion of the annual variability in egg to smolt survival  
214 (McGinnity et al. 2009), so this was added to the analysis (Fig. 2). Although not included in  
215 the analysis, the sea trout population of Burrishoole was profoundly impacted by a sharp

216 decline in marine survival in the late 1980's, and these data are presented in Fig. 2 for  
217 information.

218

219 *Statistical analysis*

220 Analyses were conducted in R, version 3.0.2 (R Core Team 2013). The SR curves for salmon  
221 and trout were modelled using linear (equation 1) or Beverton Holt models (equation 2)  
222 (Beverton and Holt 1957), with best fit being ascertained by minimising the sum of the  
223 squared residuals, where  $R$  signifies recruits (smolts),  $S$  signifies the number of eggs and  $m$ ,  $a$   
224 and  $b$  are coefficients. .

225

*Linear model:*  $R = mS$  (Equation 1.)

*Beverton Holt model:*  $R = \frac{aS}{1 + bS}$  (Equation 2.)

226

227 The residuals (observed – predicted values for each year) were extracted from the SR curves  
228 and used as the indicators of survival for each cohort of salmon and trout (Fig. 2). Salmon and  
229 trout survival were analysed with the suite of explanatory variables in order to assess possible  
230 relationships between fish stocks and environmental change. Generalized additive models  
231 (GAM) were used to assess trends in the fish data and model relationships with explanatory  
232 variables using the mgcv package (Wood 2006). As correlation amongst fish recruitment and  
233 environmental data is common (Pyper and Peterman 1998), VIFs (variance inflation factors)  
234 less than 3 were used to exclude closely related variables (Montgomery and Peck 1992, Zuur  
235 et al. 2009). All models were tested for violations of the assumptions of homogeneity,  
236 independence and normality, and amended as appropriate. Models were also examined for the  
237 effects of autocorrelation in residuals by plotting the autocorrelation function (acf) (Venables

238 and Ripley 2002) from the R Stats package (R Core Team 2013). The significance of  
239 explanatory variables were assessed using changes in the AIC (Akaike Information Criteria),  
240 explained deviance and significant F-tests comparing models with and without the variable of  
241 interest. As the temporal resolution of the land use change proxy (*LOI*) was lower than that of  
242 all other variables, models were initially fitted to the full fish datasets using all explanatory  
243 variables apart from *LOI* (salmon n=37, trout n=35) to determine the most important drivers  
244 over the time period. Subsequently *LOI* was included in the model, but using a reduced  
245 dataset (n=26 for salmon and n=11 for trout) to determine whether land use change explained  
246 some of the variation in salmonid freshwater survival.

247

## 248 **Results**

### 249 *Salmon*

250 The SR curve for salmon was best described by a linear relationship, with no obvious curve  
251 at higher spawner levels (Fig. 3). This indicates that the existing level of the monitored  
252 salmon stock in Burrishoole populates the lower end of the stock recruitment model – well  
253 away from the descending (e.g. Ricker) or flat topped (e.g. Beverton Holt) limb of a SR curve  
254 (Solomon 1985). Apart from some high values in the early 1970s, spawning in the catchment  
255 constituted between 500,000 and 2,000,000 eggs, with a corresponding smolt output of 5000  
256 and 10000 fish. This equates to an egg to smolt survival of between 0.2 and 1.2 %. The  
257 lowest survival (0.2%) was for the 1989 cohort, when an egg deposition of 1.86 million eggs  
258 led to a smolt output of only 3794 smolts.

259 The best model describing salmon freshwater survival over the study time period  
260 included the proportion of hatchery fish in the spawning cohort (*hatcheryprop*) and the NAO  
261 index (*nao*) (Table 1). This model explained 68% of the deviance in the response variable  
262 (n=37). The same model fitted to a reduced dataset (excluding *LOI*) had an explained

263 deviance of 80% and an AIC of 464. The addition of the land use change explanatory  
264 variable *LOI* to the model increased the explained deviance from 80% to 84%, but the AIC  
265 only decreased from 464 to 462, and dropping the *LOI* variable from the model was not  
266 significant when analysed using an F-test ( $p=0.12$ ) (Table 2). Taken together, these results  
267 provide sufficient evidence to conclude land use change had no significant impact on salmon  
268 survival. Higher freshwater survival was evident when the proportion of hatchery fish in the  
269 cohort was low and when the hatch year (i.e. eggs in the gravel) of the cohort coincided with  
270 a negative NAO index (cold dry winters) (Fig. 4).

271

## 272 *Trout*

273 The stock recruitment curve for anadromous trout was best described by a Beverton-Holt  
274 curve (Fig. 3). There is a clear change in the stock recruitment relationship of trout after  
275 1989/1990, with all the pre 1990 cohorts populating the upper right hand side of the curve.  
276 From 1990 on, all the cohorts are tightly grouped on the upward ascending limb in the bottom  
277 left of the curve. Average egg to smolt survival was 0.53% for the hatch years 1972 to 1989,  
278 and 1.43% for the hatch years 1990 to 2006. Before 1990, egg deposition rates ranged  
279 between *circa* 350,000 and 1,600,000 eggs, corresponding to a smolt output of 2,000 to 6,000  
280 fish. From 1990 onwards, the egg deposition of anadromous trout averaged only 70,000, and  
281 the smolt output dropped to less than 1,000 fish. The variability in the residuals from the  
282 Beverton-Holt SR curve (i.e. the trout survival index) was much higher in the earlier part of  
283 the time series, and stabilised from 1990 onwards (Fig. 2). This change in the dynamics of the  
284 trout population was fundamentally linked with decreasing marine survival, with returns of  
285 sea trout averaging 40% until 1989, but only 11% thereafter (Fig. 2).

286 A model including the water temperature in spring of the hatch year (*sprwt*) and the  
287 NAO index (*nao*) explained 79% of the deviance in the trout survival over the whole series

288 (1972-2006) (Table 3). The relationship between spring water temperature and survival was  
289 not linear, with survival decreasing as spring water temperatures increased from 6°C to 8°C  
290 but then increasing slightly as temperatures rose to 10°C (Fig. 5). The relationship between  
291 survival and the NAO index was also non-linear, with survival decreasing as the NAO index  
292 moved from a strongly negative phase towards a value of 1, but then rising again as the NAO  
293 shifted to positive values of 3. On further analysis, the non-linear nature of the relationships  
294 between trout survival, *sprwt* and *nao* appear to be an artefact of combining the two distinct  
295 phases in the Burrishoole trout population in the analysis, before and after the sea trout  
296 collapse in 1989/1990. When data from after 1989 are excluded from the analysis, the  
297 relationships between trout survival, *sprwt* and *nao* are much clearer (Fig. 6). Survival  
298 decreased as *sprwt* increased from 6 to 9 °C, and also decreased as *nao* moved from negative  
299 to positive phases. The GAM of this smaller data set had an explained deviance of 88%  
300 (n=18), and the smoothers for *sprwt* and *nao* are significant at  $p < 0.05$ . The addition of the  
301 catchment change proxy *LOI* did not increase the explained deviance of this reduced model  
302 (Table 4), although it should be noted that the sample size was very small at this stage, owing  
303 to the lower temporal resolution of the *LOI* data (n=11). However, the residuals from the full  
304 model (Table 3) also show no relationship with *LOI* over the time period 1972-2006,  
305 strengthening the conclusion that land use change had little or no impact on trout survival.  
306 Any attempt to model freshwater trout survival in the years after 1990 proved unsuccessful, a  
307 reflection of the very small amount of variation in freshwater survival during this period.

308

309

### 310 **Discussion**

311 Land use changes have had a significant impact on the ecological quality of downstream  
312 lakes in Burrishoole (Dalton et al. 2014). Remains of diatoms preserved in sediments indicate

313 increased productivity in catchment lakes, Feeagh and Bunaveela, between 1970 and 2007.  
314 The rate of sediment accumulation in the lake, linked largely to peat erosion and organic  
315 matter deposition, also increased substantially over the same period. Excessive sedimentation  
316 of headwater streams and spawning gravels is known to have adverse effects on salmonids  
317 (Soulsby et al. 2001, Suttle et al. 2004) but this does not seem to have been the case in  
318 Burrishoole. There are two possible reasons for this. First, the topography of the catchment  
319 may promote rapid wash out of eroded sediment from upland spawning streams. Rivers in the  
320 catchment are characterised by high frequency spates, with floods rising within an hour of  
321 rainfall events, and frequent high water levels throughout the year. This was accentuated  
322 when ground preparation for afforestation, including extensive land drainage networks, was  
323 carried out in the mid-20<sup>th</sup> century (Müller 2000). Thus the main sediment deposition could  
324 have occurred in the standing waters of Bunaveela and Feeagh, rather than in the headwater  
325 streams where salmonid spawning takes place. Second, increased productivity in the  
326 catchment may have benefited the salmon population: even slight increases in nutrients  
327 (carbon, nitrogen or phosphorus) in catchment lakes may have resulted in greater food  
328 availability to salmon. Graham et al. (2014) noted that trout found in Irish lakes situated in  
329 afforested catchments were larger than those found in un-afforested catchments. This  
330 observation was attributed to eutrophication of small lakes by commercial forestry actions  
331 including fertilisation of recently planted conifer crops, accelerated peat decomposition,  
332 mineralisation of disturbed peatlands, and increased availability of organic matter from  
333 felling residues (Drinan et al. 2013). Similarly, organic matter from forested catchments was  
334 found to enhance bacterial biomass, and hence supply extra energy through the food web of  
335 Canadian lakes, boosting the biomass of planktivorous fish (Tanentzap et al. 2014). Additions  
336 of leaf litter and terrestrial invertebrates from forestry can also positively impact on  
337 productivity (Wipfli 1997, Wallace et al. 1997, Dineen et al. 2007), by increasing the



338 allocthonous energy supply to fish and hence the enriching riverine salmon populations  
339 (Johansen et al. 2005). The results of this study indicate that there was no impact of the land  
340 use changes in Burrishoole on salmonid survival, either positive or negative.

341         There were no data available describing salmon survival before 1970, nor were there  
342 data to show whether the number of returning adults described here was particularly high or  
343 low relative to previous decades. There is, thus, no way of ascertaining whether the period  
344 described in this paper is representative of the historical number of salmon spawning in the  
345 catchment, or historical freshwater survival. Our time series represents a general period of  
346 decline in the number of Atlantic salmon in the North Atlantic (Limburg and Waldman 2009)  
347 following a productive period between 1950 and 1970, with high commercial catches (Parrish  
348 et al. 1998, Boylan and Adams 2006). Local evidence suggest that salmon numbers were  
349 much higher in Burrishoole during that time period, with reported draft net catches in Lough  
350 Furnace (a coastal lagoon downstream of Lough Feeagh and the fish traps) of 500 grilse and  
351 120 MSW (multi-sea winter) salmon in the early 1950s (Nixon 1999). For comparison, the  
352 total returns through the Burrishoole traps for the period 1970-2006 averaged 518 grilse and  
353 19 MSW fish. The linear nature of the SR curve for salmon indicates that the current stock  
354 (i.e. the last five decades) does not exhibit a compensatory relationship, and it seems likely  
355 that the catchment could support a much larger population of salmon, without affecting  
356 density dependant survival, should stocks improve in the future. It is possible that the period  
357 1971-1995 represented a low level of salmon survival coinciding with land use change and a  
358 deleterious hatchery influence, with 1995-2007 representing a recovery of sorts. Whatever  
359 the mechanism behind the observed increase in freshwater survival in salmon, no significant  
360 *negative* impact of land use changes on salmon stocks in freshwater is evident. However,  
361 caution must be applied to any conclusions based on this result. Although the Burrishoole  
362 catchment has become more trophically enriched over the period discussed here, it remains

363 oligotrophic. Openwater phosphorus levels in Lough Feeagh rarely exceed  $10\mu\text{gL}^{-1}$  and  
364 chlorophyll *a* values are generally less than  $2\mu\text{gL}^{-1}$  (Marine Institute, unpublished data),  
365 putting the lake into the oligotrophic category (after Carlson 1977). The humic nature of the  
366 waters in Lough Feeagh may limit autotrophic primary production, even with increased  
367 nutrients (P and N) (Karlsson et al. 2009, Sparber et al. 2015). In addition, long term  
368 monitoring of some of the rivers in the catchment by the Irish Environmental Protection  
369 Agency indicates that water quality is still good (McGarrigle et al. 2011), with Q-indices of 4,  
370 4-5 and 5. The Q index is an Irish rating system used to classify river water quality against a  
371 trophic gradient, with Q5 sites showing no signs of eutrophication, while Q1 sites are  
372 severely affected (Toner et al. 2005). Work by Kelly et al. (2007) indicates that salmonid  
373 populations begin to be impacted once river sites fall below Q4.

374 The salmon model presented in this paper is an extension of work described in  
375 McGinnity et al. (2009), which found that 76% of the interannual variability in egg-to-smolt  
376 survival was related to a set of climatic and management related (% hatchery fish) drivers. At  
377 the time of that analysis, land use change proxies were not available for inclusion, but were  
378 acknowledged to be a likely source of variation. In addition, the survival index used in  
379 McGinnity et al. (2009) (egg to smolt survival) did not take account of the density dependant  
380 nature of the relationship between survival and spawning stock size. Nevertheless, the results  
381 presented here support the conclusions of this previous analysis, and confirm that, together  
382 with climatic variables, the influence of hatchery fish in the spawning cohort accounts for a  
383 large proportion of the variability in salmon survival in Burrishoole. The addition of a land  
384 use change proxy (*LOI*) did not explain any additional variation in the dataset, but underlines  
385 the importance of considering multiple drivers in any assessment of long term directional  
386 changes in stock recruitment relationships.

387 The dynamics of the anadromous trout population in Burrishoole was profoundly

388 affected by changing conditions at sea in the late 1980s, leading to poorer returns of potential  
389 spawners to the catchment. This meant that any impact of environmental disturbance in  
390 freshwater was going to be difficult to detect. Trout could be expected to respond to increased  
391 productivity in the catchment in a similar fashion to that described for salmon but there is  
392 little evidence for this in Burrishoole. The trout population after 1989 bore little resemblance  
393 to that of the 1970s and 1980s, with the number of migratory trout falling by an order of  
394 magnitude from an average of 2,624 between 1975-1979, to an average of 115 between 2000  
395 and 2003 (Poole et al. 2006). While smolt output decreased substantially after 1989, egg to  
396 smolt survival actually increased. Relaxation of density dependence on juvenile trout may be  
397 responsible for this increase in freshwater survival. It is, however, also possible that it is due  
398 to an increased relative contribution of resident trout to smolt output, although this is thought  
399 to be low (Poole et al. 2006). The stock–recruitment relationship for Burrishoole migratory  
400 trout suggests that the production of smolts, or juvenile recruits, is closely related to the level  
401 of ova deposited by migratory trout, supporting the hypothesis that the propensity for marine  
402 migration is under strong genetic control, and the increase in egg-smolt survival post 1989 is  
403 a real phenomenon of the anadromous portion of the trout population (Poole et al. 2006).

404         The relationship between the NAO index and egg-smolt survival of both trout and  
405 salmon is interesting, but not unexpected. Negative NAO index values are accompanied by  
406 cold, dry and calm winters in northwest Europe, whereas positive values are correlated with  
407 milder winters, strong westerly winds and higher rainfall (Hurrell 1995). Such variation in  
408 precipitation and temperature, at a time when salmonids are spawning and emerging as  
409 vulnerable swim-up fry, is expected to bring about significant variation in survival. Previous  
410 studies have highlighted the impact of NAO on aquatic ecosystems in western Europe  
411 (Weyhenmeyer et al. 1999, Bradley and Ormerod 2001, Straile et al. 2003), including the  
412 Burrishoole (Jennings et al. 2000, Blenckner et al. 2007), and also on the fish populations

413 native to these catchments (Elliott et al. 2000, Kallio-nyberg et al. 2004, Alonso et al. 2011).  
414 Results presented in this paper show that even in combination with many other pressures, the  
415 NAO influence on survival of salmon and trout in freshwater is significant. Salmonid survival  
416 is highest when the NAO index is negative, i.e. when winters are cold, dry and calm. As this  
417 NAO link is apparent for the hatch year, we interpret these results as the impact of winter  
418 weather on cohorts hatching from the stream gravels and emerging as fry. Possible reasons  
419 for this relationship include wash out of eggs and fry from gravels in wet winters (Jensen and  
420 Johnsen 1999), or a mismatch in developmental schedules in warm winters between the  
421 hatching eggs and emerging fry and their prey, resulting in insufficient energy reserves for  
422 survival (McGinnity et al. 2009, Jonsson and Jonsson 2011). Future climate projections for  
423 the Atlantic coast of Europe (Beniston et al. 2007) and specifically for Burrishoole (Fealy et  
424 al. 2014) include an increase in winter rainfall, and warmer winter temperatures. Results from  
425 this study indicate that the occurrence of such changes could be detrimental to freshwater  
426 survival of salmon and trout. A step change in air temperature which occurred in Ireland and  
427 across Europe in 1987–1988 has been attributed to the start of an extended positive phase of  
428 the NAO and has been associated with ecological changes (Beaugrand 2004, Fealy and  
429 Sweeney 2005, Donnelly et al. 2009), including an increase in the incidence of disease in  
430 brown trout *Salmo trutta* in Switzerland (Hari et al. 2006).

431         The impact of spring water temperatures on trout survival appears to be stronger than  
432 the influence of winter climate as indicated by NAO. Spring water temperatures will  
433 invariably be higher after winters with positive NAO indices, especially if water temperatures  
434 are measured in lakes that may take several months to warm or cool. Thus, the two variables  
435 are interlinked. Nevertheless, spring water temperature and NAO were not strongly correlated  
436 in this study, indicating that warm spring weather puts an additional stress on trout in  
437 freshwater that is not apparent for salmon. More detailed analysis using juvenile trout

438 densities may help to elucidate the mechanism between spring water temperature and  
439 survival. The causes are likely to be similar to those outlined above with reference to winter  
440 temperatures.

441 In conclusion, the data reported here underline the importance of maintaining long  
442 term datasets against which to test long held hypotheses, and to generate knowledge of  
443 ecosystem processes sufficient to understand the likely consequences of human actions  
444 (Pikitch et al. 2004). Diadromous fish are particularly at risk from multiple impacts in  
445 marine, transitional and freshwater environments as well as the overarching impact of climate  
446 change. Understanding the relative importance of these impacts allows managers to make  
447 informed decisions on the measures required to conserve these stocks. In Burrishoole, the  
448 most important determinant of freshwater survival of salmon was the deleterious effect of  
449 hatchery fish in the spawning cohort for salmon. While stocking is seen by many as a  
450 possible management action to conserve and bolster stocks, evidence continues to mount that  
451 where a wild population is present, and habitat is available, stocking is misguided  
452 (McGinnity et al. 2009, Bacon et al. 2015). The impact of reduced marine survival as a result  
453 of sea lice parasitism (Poole et al. 1990, Gargan et al. 2006, Thorstad et al. 2015) on the  
454 Burrishoole migratory trout was very significant, and transformed the dynamics of the  
455 population. Any relationship with land use change was likely to pale into insignificance in  
456 comparison, and we found this to be the case. In the case of salmonids, direct anthropogenic  
457 impacts, which in hindsight could have been avoided or minimised, have posed the greatest  
458 risk to the conservation of stocks in Burrishoole, notwithstanding the significant influence of  
459 climatic factors. The lesson to be learned here must surely be to minimise those impacts that  
460 we now know are likely to affect stocks of diadromous fish, with the knowledge that there are  
461 many unpredictable and less easily controlled confounding effects on the horizon. Finally, the  
462 role that an ecosystem approach using long term ecological monitoring must play in

463 providing the evidence needed to manage diadromous fish stocks cannot be underestimated.

464

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473

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- 750

751 **Table 1.** Generalized additive model of salmon freshwater survival in the Burrishoole  
 752 catchment. Variables included were *nao*: NAO - Hurrells winter index and *hatcheryprop*:  
 753 proportion of hatchery fish in the spawning escapement. Deviance explained = 68%, R-  
 754 sq.(adj) = 0.58, GCV score < 0.001, Scale est. < 0.001 and n = 37

Parametric coefficients	Estimate	Std. Error	t-value	<i>p</i>
Intercept	680.4	274.8	2.5	0.02
Approximate significance of smooth terms	edf	Ref.df	F	<i>p</i>
<i>s(nao)</i>	5.4	6.5	2.6	0.03
<i>s(hatcheryprop)</i>	2.9	3.5	4.2	0.01

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756

757 **Table 2.** Generalized additive models of salmon freshwater survival in the Burrishoole  
 758 catchment. Variables included were *nao*: NAO - Hurrells winter index; *LOI* : loss on ignition  
 759 of sediment from L. Feeagh; *hatcheryprop*: proportion of hatchery fish in the spawning  
 760 escapement. The value of Pr(>F) gives the significance of dropping one term from model 1,  
 761 by comparing the difference in deviances of the nested models using an F-test. n= 26 for all  
 762 models.

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Model	AIC	Explained deviance	Pr(>F)
1. <i>Survival ~ s(hatcheryprop) + s(nao)+LOI</i>	462	84%	
2. <i>Survival ~ s(hatcheryprop) + s(nao)</i>	464	80%	0.12
3. <i>Survival ~ s(hatcheryprop) +LOI</i>	474	61%	0.01
4. <i>Survival ~ LOI+s(nao)</i>	476	61%	0.006

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767 **Table 3.** Generalized additive model of trout freshwater survival in the Burrishoole  
 768 catchment. Variables included were *sprwt*: average water temperature for spring (Mar, Apr,  
 769 May) of hatch year, and *nao*: NAO - Hurrells winter index. Deviance explained = 79%, R-  
 770 sq.(adj) = 0.67, GCV score < 0.001, Scale est. =78166 and n = 35

Parametric coefficients	Estimate	Std. Error	t-value	<i>p</i>
Intercept	-7.36	47.26	-0.16	0.87
Approximate significance of smooth terms	edf	Ref.df	F	<i>p</i>
<i>s(sprwt)</i>	7.61	8.42	6.36	<0.0001
<i>s(nao)</i>	5.34	6.41	2.64	0.04

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774 **Table 4.** Generalized additive models of trout freshwater survival in the Burrishoole  
 775 catchment for years between 1972 and 1989. Variables included were *sprwt*: average water  
 776 temperature for spring (Mar, Apr, May) of hatch year; *nao*: NAO - Hurrells winter index and  
 777 *LOI* : loss on ignition of sediment from L. Feeagh. The value of Pr(>F) gives the significance  
 778 of dropping one term from model 1, by comparing the difference in deviances of the nested  
 779 models using an F-test. n= 11 for all models.

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Model	AIC	Explained deviance	Pr(>F)
<i>Survival</i> ~ <i>s(sprwt)</i> + <i>nao</i> + <i>LOI</i>	169	61%	
<i>Survival</i> ~ <i>s(sprwt)</i> + <i>nao</i>	166	61%	0.96
<i>Survival</i> ~ <i>s(sprwt)</i> + <i>LOI</i>	167	59%	0.61
<i>Survival</i> ~ <i>nao</i> + <i>LOI</i>	174	17%	0.02

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780

781 Figure legends

782

783 Fig. 1. Map of the Burrishoole catchment, showing its location in Ireland. © Ordnance  
784 Survey Ireland Discovery Series. EPA and MI data provided under Creative Commons  
785 CC-BY 4.0 licence.

786 Fig. 2. Fish response variables (salmon and trout survival), the land use change proxy  
787 (*LOI*), climatic (teleconnections, temperature, precipitation) and other explanatory  
788 variables (influence of hatchery stocks and marine survival) considered in the analysis.  
789 Additional seasonal climatic variables were included (winter, summer and autumn values  
790 of water temperature and precipitation), but are not plotted.

791 Fig. 3. Stock recruitment curves for salmon (left) and trout (right) from the Burrishoole  
792 catchment. Dotted lines indicate the best fit SR curve. For salmon:  $R^2= 89\%$ ,  $m=6352$   
793 (eq.1). For trout:  $R^2= 80\%$ ,  $a=18087$ ,  $b=3.312$  (eq. 2). See main text for equation details.

794 Fig. 4. Conditional plots of partial residuals for each explanatory variable in a GAM  
795 describing salmon freshwater survival in the Burrishoole catchment (details in Table 1.).  
796 The lines indicate mean model fit  $\pm 95\%$  c.i.'s in shaded polygons. These plots shows the  
797 value of the explanatory variable of interest (x-axis), and the change in the response  
798 variable (y-axis), holding all other variables constant.

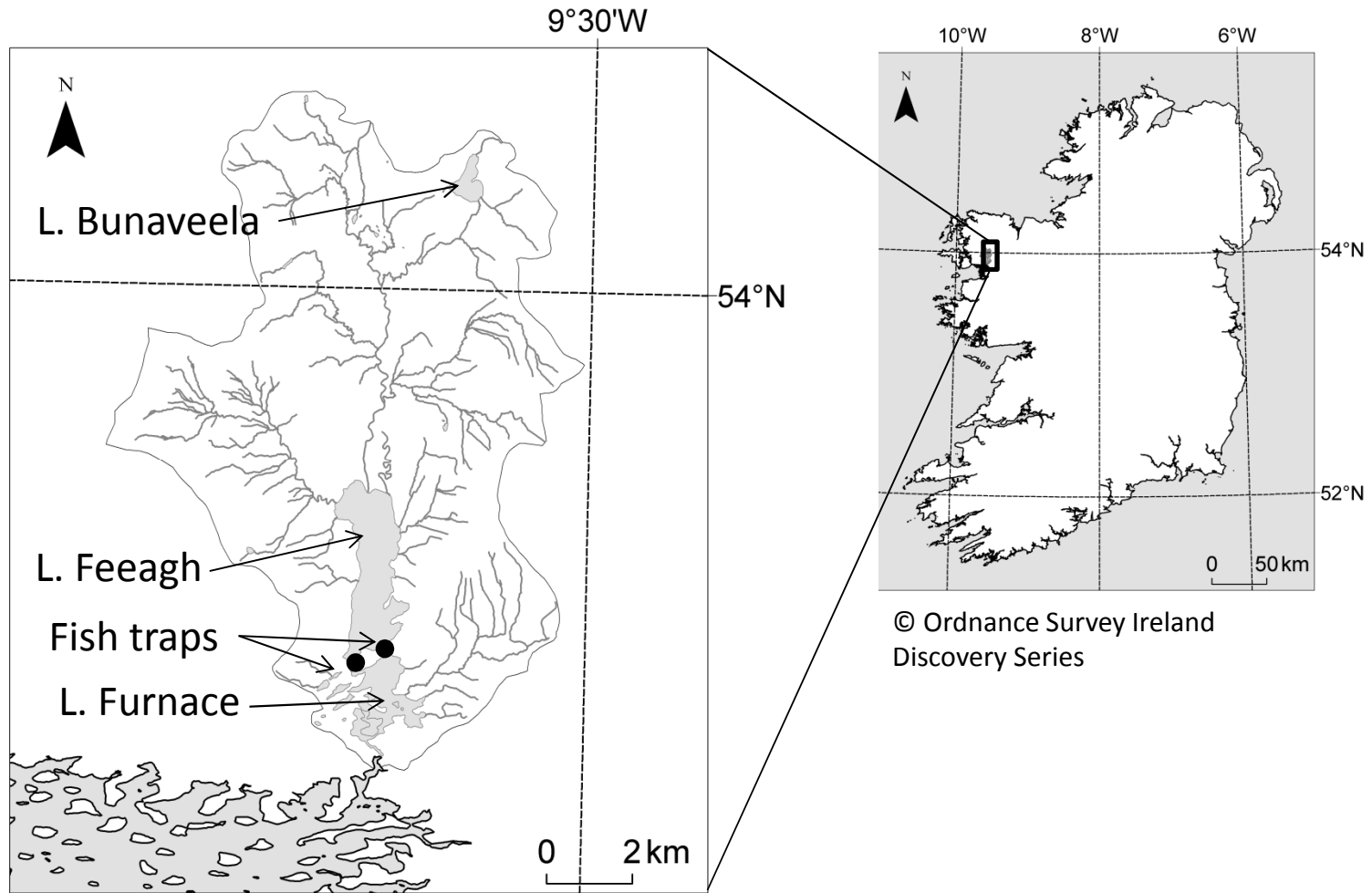
799 Fig. 5. Conditional plots of partial residuals for each explanatory variable in a GAM  
800 describing trout egg-smolt freshwater survival in the Burrishoole catchment (see table 3)  
801 between 1972 and 2006. The lines indicate mean model fit  $\pm 95\%$  c.i.'s in shaded  
802 polygons.

803 Fig. 6. Conditional plots of partial residuals for each explanatory variable in a GAM

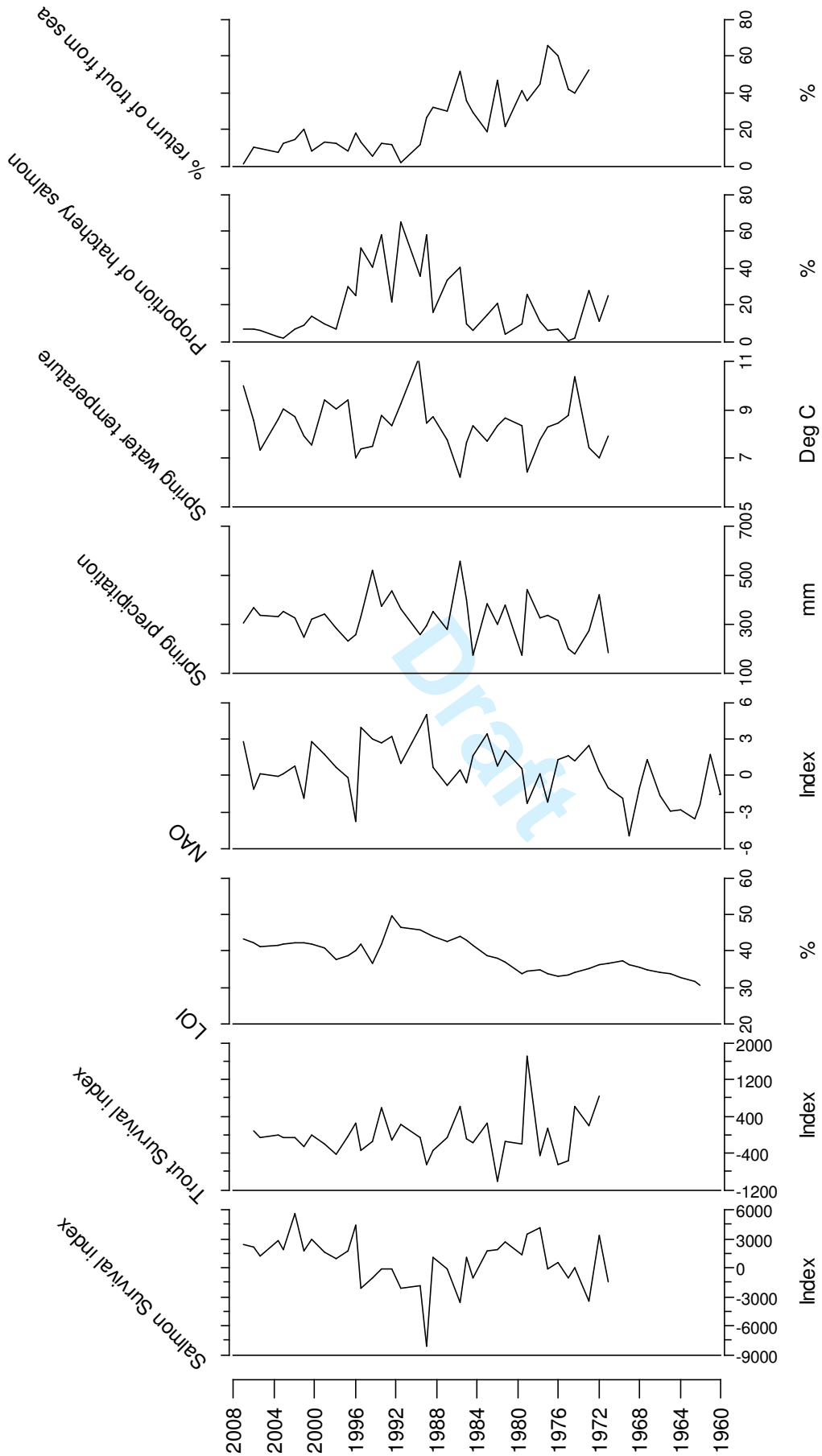
804 describing trout egg-smolt freshwater survival in the Burrishoole catchment between  
805 1972 and 1989. The lines indicate mean model fit  $\pm$  95% c.i.'s in shaded polygons.

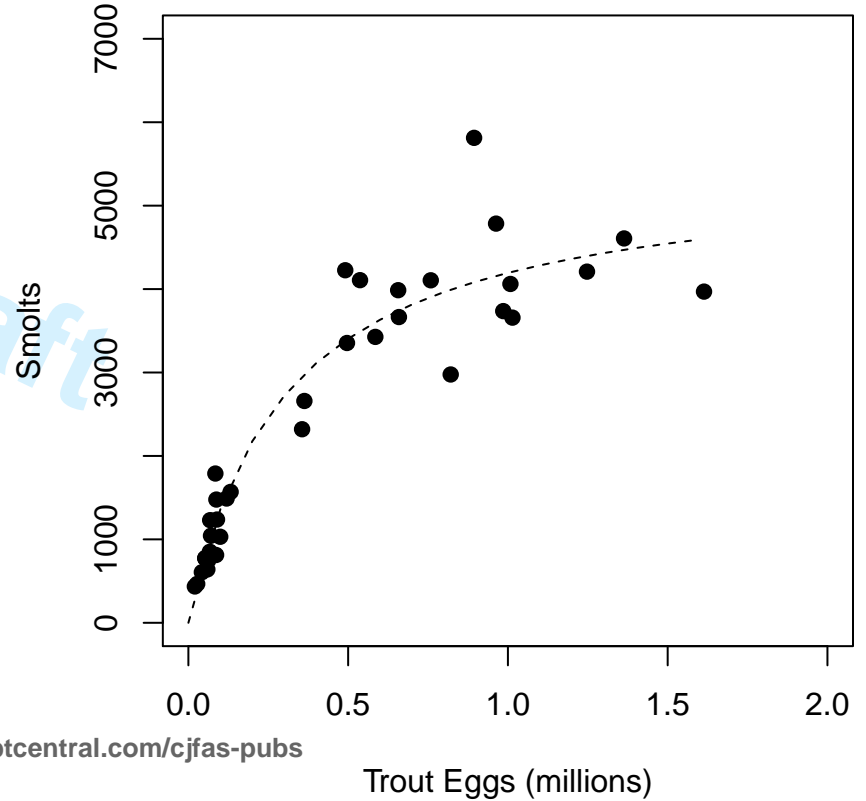
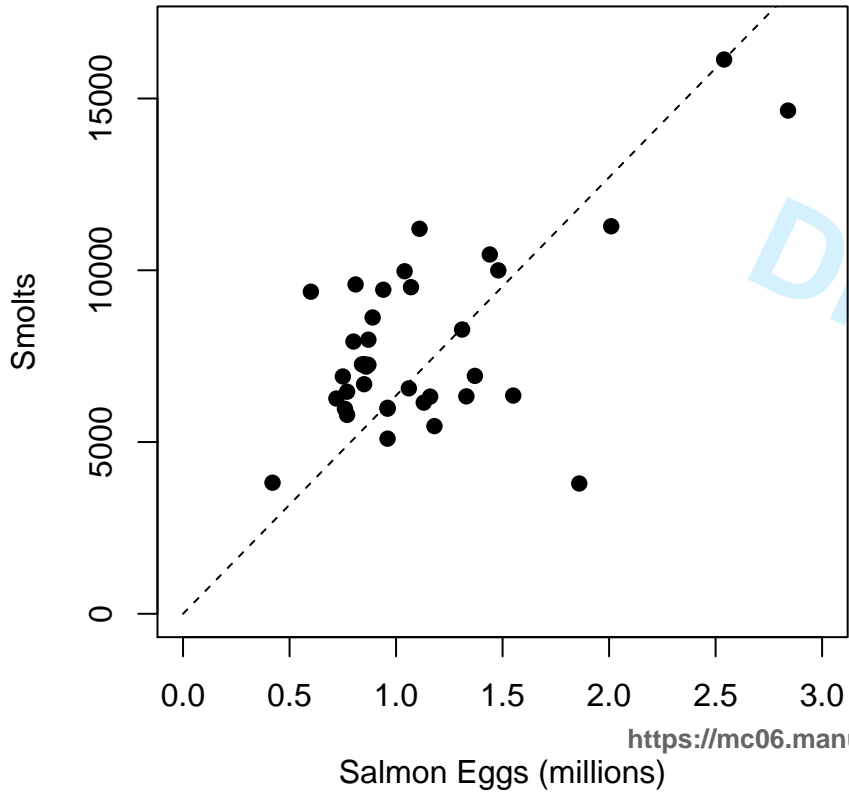
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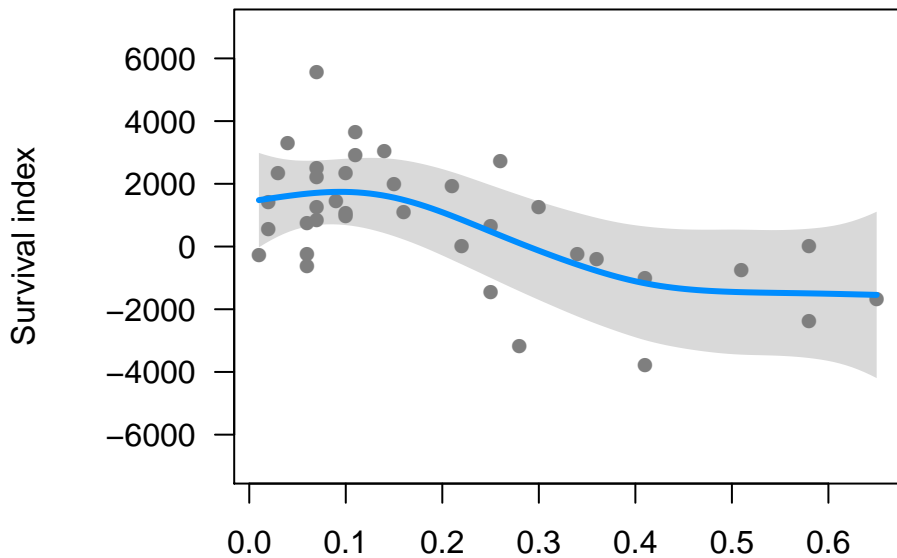
Draft











Proportion of hatchery fish in spawning cohort

