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

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Abstract

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

Introduction

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

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

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

Atlantic salmon and anadromous brown trout are native to the Burrishoole catchment in the west of Ireland. At these latitudes, Atlantic salmon and anadromous trout spawn in winter and spend 1-4 years in freshwater before entering the sea as smolts (Metcalfe and Thorpe 1990). They return to their natal rivers to spawn after one or more years. A long-term monitoring programme of migrating salmon and trout has enabled quantification of key trends in the Burrishoole diadromous fish populations from the 1960s to the present. In addition to the long-term fish population records, a detailed reconstruction of aquatic ecosystem responses to land use change in the Burrishoole in the 20th century is available (Dalton et al. 2014). This palaeolimnological reconstruction was described from a sediment core taken from the deepest point of Lough Feeagh, the most downstream lake in the Burrishoole catchment. Slices of this core were dated and analysed for commonly used palaeolimnological proxies, which enabled the key land use changes in the catchment to be quantified and dated.   Low nutrient levels prevailed in the lakes in the catchment lakes until the 1950s. Commercial coniferous afforestation in the mid-20th century and extensive sheep overgrazing in the 1980s and 1990s (Gillmor and Walsh 1993) were associated with increased rates of erosion, leading to elevated sedimentation, organic matter and nutrients in downstream lakes, and a shift to mesotrophic conditions (Dalton et al. 2014). This reconstruction provided valuable information that captured the degradation of the lake and its water catchment along a trajectory spanning the last century that is representative of many upland peat catchments on the Atlantic coast of Ireland (Huang and O'Connell 2000, Bullock et al. 2012) and beyond (Evans et al. 2014). In these catchments, afforestation and overgrazing have been a focus of fisheries and aquatic ecosystems conservation efforts (Fitzsimons and Igoe 2004, Drinan et al. 2013, Harrison et al. 2014).

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

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

Materials and Methods

Site description

Burrishoole is a small (100 km^2) upland catchment (53° 56' N, 9° 35' W) draining into the North-east Atlantic through Clew Bay (Fig. 1). Climatically influenced by the Atlantic Ocean (Jennings et al. 2000, Allott et al. 2005, Blenckner et al. 2007), the catchment experiences a temperate, oceanic climate with mild winters and relatively cool summers. Maximum summer air temperatures rarely exceed 20°C, while minimum winter temperatures are usually between 2°C and 4°C. The base geology on the western side of the catchment is predominantly quartzite and schist, leading to acidic runoff, with poor buffering capacity. By comparison, the geology on the eastern side is more complex as quartzite and schist are interspersed with veins of volcanic rock, dolomite and wacke, leading to higher buffering capacity and aquatic production. Soils in the catchment comprise poorly drained gleys, peaty podsols and blanket peats. Feeagh and Bunaveela, the two largest freshwater lakes in the catchment, are both relatively deep (mean depth >12 m), oligotrophic (TP <10 ug l^{-1}), coloured (c. 80 mg l^{-1} PtCo) due to high levels of dissolved organic carbon (DOC), have low alkalinity (<20 mgl^{-1} $CaCO_3$) and are slightly acidic (pH = c. 6.7).

Partial upstream and downstream fish trapping facilities have been in operation in Burrishoole since 1958, and full trapping facilities were put in place in 1970. The traps enable a complete census of migrating fish in (adult salmon and sea trout) and out (salmon and trout smolts) of the catchment. A variable number of individuals from a captive bred population of salmon (‘Burrishoole hatchery fish’) were released upstream of the traps during the study period, and spawned along with the wild population. Census details are recorded in the annual reports of the research station (e.g. Marine Institute 2013). A rod fishery for salmon and trout operated during the time period of interest, between June and September of each year. The salmon and sea trout catches have changed considerably since the 1970s. For example, the average number of salmon and sea trout caught in the period 1970-74 (including wild and hatchery fish) was 237 and 967 respectively. In 1996, the salmon catch was 295 but the sea trout catch had dropped to 125. Since 1995, all wild salmon fishing has been on a catch and release basis, with restrictions on fishing on Feeagh imposed for conservation reasons. Data from these fisheries are included in the census data where relevant (e.g. fish which were caught and released are including in the spawning escapement, while fish killed are not).

Data collation

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

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

Land use change explanatory variables (n=14) were extracted from the analysis described in Dalton et al. (2014). As many of these explanatory variables were highly collinear, initial data exploration was used to extract a land use change proxy which adequately reflected the timing and direction of impacts on the downstream aquatic ecosystem (Lough Feeagh) (Fig. 2). Percentage loss on ignition (*LOI*) was measured at 1cm intervals from the Lough Feeagh core (Dalton et al. 2014). *LOI* quantifies changes in the proportion of organic material in sediment accumulating in the lake (Heiri et al. 2001). In an oligotrophic lake in a catchment that is largely blanketed in peat, major changes in the proportion of organic material in sediments are likely to represent variations in external loadings to the lake, as a result of peat erosion and inwash. *LOI* can therefore be used as a proxy of catchment instability. The proportion of organic matter increased from baseline conditions of ~ 27% before 1960, and rose to 46% by the mid-1990s. It then decreased to ~40% after 2000. Twenty-six samples from the Lough Feeagh core were analysed for *LOI* in the time period for which salmonid data were available (1971-2007) and were matched to the relevant hatch year using a Constant Rate of Supply (CRS) model for determining accumulation rates (Appleby 2002). CRS estimates were validated with reference to 137Cs fallout chronostratigraphic markers (1986 Chernobyl and 1963 weapons testing).

While the aim of this paper was to estimate the role that land use change has played in the population dynamics of fish in Burrishoole, previous research has highlighted several climatic and other factors (Fig. 2) accounting for some of the observed variation in Burrishoole salmon and trout trends (McGinnity et al. 2009). Water temperature was measured adjacent to the fish trap on the eastern outflow from Lough Feeagh (Fig. 1) using a paper chart recorder. Data were extracted at midnight for each day, and averaged to produce seasonal values (winter – Dec, Jan, Feb; spring – Mar, Apr, May; summer – Jun, Jul, Aug; autumn – Sep, Oct, Nov) (Fig. 2). Similarly, precipitation measured at the Burrishoole manual weather station (Fig. 1) was expressed as seasonal accumulations of daily rainfall (Fig. 2). Both Dalton et al. (2014) and Jennings et al. (2000) highlighted the correlation between the NAO index and catchment responses in the Burrishoole, and so this index was included as a potential climatic explanatory variable (average values for the months of December, January, February, and March: Hurrells winter Index (Hurrell 1995) (Fig. 2). Previous analysis of the freshwater survival of salmon in Burrishoole has shown that the proportion of hatchery fish in the spawning cohort (which varied between 1 and 60% over the time series), accounted for a large proportion of the annual variability in egg to smolt survival (McGinnity et al. 2009), so this was added to the analysis (Fig. 2). Although not included in the analysis, the sea trout population of Burrishoole was profoundly impacted by a sharp decline in marine survival in the late 1980's, and these data are presented in Fig. 2 for information.

Statistical analysis

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

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

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

The residuals (observed – predicted values for each year) were extracted from the SR curves and used as the indictors of survival for each cohort of salmon and trout (Fig. 2). Salmon and trout survival were analysed with the suite of explanatory variables in order to assess possible relationships between fish stocks and environmental change. Generalized additive models (GAM) were used to assess trends in the fish data and model relationships with explanatory variables using the mgcv package(Wood 2006). As correlation amongst fish recruitment and environmental data is common (Pyper and Peterman 1998), VIFs (variance inflation factors) less than 3 were used to exclude closely related variables (Montgomery and Peck 1992, Zuur et al. 2009). All models were tested for violations of the assumptions of homogeneity, independence and normality, and amended as appropriate. Models were also examined for the effects of autocorrelation in residuals by plotting the autocorrelation function (acf) (Venables and Ripley 2002) from the R Stats package (R Core Team 2013). The significance of explanatory variables were assessed using changes in the AIC (Akaike Information Criteria), explained deviance and significant F-tests comparing models with and without the variable of interest. As the temporal resolution of the land use change proxy (*LOI*) was lower than that of all other variables, models were initially fitted to the full fish datasets using all explanatory variables apart from *LOI* (salmon n=37, trout n=35) to determine the most important drivers over the time period. Subsequently *LOI* was included in the model, but using a reduced dataset (n=26 for salmon and n=11 for trout) to determine whether land use change explained some of the variation in salmonid freshwater survival.

Results

Salmon

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

The best model describing salmon freshwater survival over the study time period included the proportion of hatchery fish in the spawning cohort (*hatcheryprop*) and the NAO index (*nao*) (Table 1). This model explained 68% of the deviance in the response variable (n=37). The same model fitted to a reduced dataset (excluding *LOI*) had an explained deviance of 80% and an AIC of 464. The addition of the land use change explanatory variable *LOI* to the model increased the explained deviance from 80% to 84%, but the AIC only decreased from 464 to 462, and dropping the *LOI* variable from the model was not significant when analysed using an F-test (*p*=0.12) (Table 2). Taken together, these results provide sufficient evidence to conclude land use change had no significant impact on salmon survival. Higher freshwater survival was evident when the proportion of hatchery fish in the cohort was low and when the hatch year (i.e. eggs in the gravel) of the cohort coincided with a negative NAO index (cold dry winters) (Fig. 4).

Trout

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

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

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

Discussion

Land use changes have had a significant impact on the ecological quality of downstream lakes in Burrishoole (Dalton et al. 2014). Remains of diatoms preserved in sediments indicate increased productivity in catchment lakes, Feeagh and Bunaveela, between 1970 and 2007. The rate of sediment accumulation in the lake, linked largely to peat erosion and organic matter deposition, also increased substantially over the same period. Excessive sedimentation of headwater streams and spawning gravels is known to have adverse effects on salmonids (Soulsby et al. 2001, Suttle et al. 2004) but this does not seem to have been the case in Burrishoole. There are two possible reasons for this. First, the topography of the catchment may promote rapid wash out of eroded sediment from upland spawning streams. Rivers in the catchment are characterised by high frequency spates, with floods rising within an hour of rainfall events, and frequent high water levels throughout the year. This was accentuated when ground preparation for afforestation, including extensive land drainage networks, was carried out in the mid-20th century (Müller 2000). Thus the main sediment deposition could have occurred in the standing waters of Bunaveela and Feeagh, rather than in the headwater streams where salmonid spawning takes place. Second, increased productivity in the catchment may have benefited the salmon population: even slight increases in nutrients (carbon, nitrogen or phosphorus) in catchment lakes may have resulted in greater food availability to salmon. Graham et al. (2014) noted that trout found in Irish lakes situated in afforested catchments were larger than those found in un-afforested catchments. This observation was attributed to eutrophication of small lakes by commercial forestry actions including fertilisation of recently planted conifer crops, accelerated peat decomposition, mineralisation of disturbed peatlands, and increased availability of organic matter from felling residues (Drinan et al. 2013). Similarly, organic matter from forested catchments was found to enhance bacterial biomass, and hence supply extra energy through the food web of Canadian lakes, boosting the biomass of planktivorous fish (Tanentzap et al. 2014). Additions of leaf litter and terrestrial invertebrates from forestry can also positively impact on productivity (Wipfli 1997, Wallace et al. 1997, Dineen et al. 2007), by increasing the allocthonous energy supply to fish and hence the enriching riverine salmon populations (Johansen et al. 2005). The results of this study indicate that there was no impact of the land use changes in Burrishoole on salmonid survival, either positive or negative.

There were no data available describing salmon survival before 1970, nor were there data to show whether the number of returning adults described here was particularly high or low relative to previous decades. There is, thus, no way of ascertaining whether the period described in this paper is representative of the historical number of salmon spawning in the catchment, or historical freshwater survival. Our time series represents a general period of decline in the number of Atlantic salmon in the North Atlantic (Limburg and Waldman 2009) following a productive period between 1950 and 1970, with high commercial catches (Parrish et al. 1998, Boylan and Adams 2006). Local evidence suggest that salmon numbers were much higher in Burrishoole during that time period, with reported draft net catches in Lough Furnace (a coastal lagoon downstream of Lough Feeagh and the fish traps) of 500 grilse and 120 MSW (multi-sea winter) salmon in the early 1950s (Nixon 1999). For comparison, the total returns through the Burrishoole traps for the period 1970-2006 averaged 518 grilse and 19 MSW fish. The linear nature of the SR curve for salmon indicates that the current stock (i.e. the last five decades) does not exhibit a compensatory relationship, and it seems likely that the catchment could support a much larger population of salmon, without affecting density dependant survival, should stocks improve in the future. It is possible that the period 1971-1995 represented a low level of salmon survival coinciding with land use change and a deleterious hatchery influence, with 1995-2007 representing a recovery of sorts. Whatever the mechanism behind the observed increase in freshwater survival in salmon, no significant *negative* impact of land use changes on salmon stocks in freshwater is evident. However, caution must be applied to any conclusions based on this result. Although the Burrishoole catchment has become more trophically enriched over the period discussed here, it remains oligotrophic. Openwater phosphorus levels in Lough Feeagh rarely exceed 10µgL^{-1} and chlorophyll *a* values are generally less than 2 µgL^{-1} (Marine Institute, unpublished data), putting the lake into the oligotrophic category (after Carlson 1977). The humic nature of the waters in Lough Feeagh may limit autotrophic primary production, even with increased nutrients (P and N) (Karlsson et al. 2009, Sparber et al. 2015). In addition, long term monitoring of some of the rivers in the catchment by the Irish Environmental Protection Agency indicates that water quality is still good (McGarrigle et al. 2011), with Q-indices of 4, 4-5 and 5. The Q index is an Irish rating system used to classify river water quality against a trophic gradient, with Q5 sites showing no signs of eutrophication, while Q1 sites are severely affected (Toner et al. 2005). Work by Kelly et al. (2007) indicates that salmonid populations begin to be impacted once river sites fall below Q4.

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

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

The relationship between the NAO index and egg-smolt survival of both trout and salmon is interesting, but not unexpected. Negative NAO index values are accompanied by cold, dry and calm winters in northwest Europe, whereas positive values are correlated with milder winters, strong westerly winds and higher rainfall (Hurrell 1995). Such variation in precipitation and temperature, at a time when salmonids are spawning and emerging as vulnerable swim-up fry, is expected to bring about significant variation in survival. Previous studies have highlighted the impact of NAO on aquatic ecosystems in western Europe (Weyhenmeyer et al. 1999, Bradley and Ormerod 2001, Straile et al. 2003), including the Burrishoole (Jennings et al. 2000, Blenckner et al. 2007), and also on the fish populations native to these catchments (Elliott et al. 2000, Kallio-nyberg et al. 2004, Alonso et al. 2011). Results presented in this paper show that even in combination with many other pressures, the NAO influence on survival of salmon and trout in freshwater is significant. Salmonid survival is highest when the NAO index is negative, i.e. when winters are cold, dry and calm. As this NAO link is apparent for the hatch year, we interpret these results as the impact of winter weather on cohorts hatching from the stream gravels and emerging as fry. Possible reasons for this relationship include wash out of eggs and fry from gravels in wet winters (Jensen and Johnsen 1999), or a mismatch in developmental schedules in warm winters between the hatching eggs and emerging fry and their prey, resulting in insufficient energy reserves for survival (McGinnity et al. 2009, Jonsson and Jonsson 2011). Future climate projections for the Atlantic coast of Europe (Beniston et al. 2007) and specifically for Burrishoole (Fealy et al. 2014) include an increase in winter rainfall, and warmer winter temperatures. Results from this study indicate that the occurrence of such changes could be detrimental to freshwater survival of salmon and trout. A step change in air temperature which occurred in Ireland and across Europe in 1987–1988 has been attributed to the start of an extended positive phase of the NAO and has been associated with ecological changes (Beaugrand 2004, Fealy and Sweeney 2005, Donnelly et al. 2009), including an increase in the incidence of disease in brown trout *Salmo trutta* in Switzerland (Hari et al. 2006).

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

In conclusion, the data reported here underline the importance of maintaining long term datasets against which to test long held hypotheses, and to generate knowledge of ecosystem processes sufficient to understand the likely consequences of human actions (Pikitch et al. 2004). Diadromous fish are particularly at risk from multiple impacts in marine, transitional and freshwater environments as well as the overarching impact of climate change. Understanding the relative importance of these impacts allows managers to make informed decisions on the measures required to conserve these stocks. In Burrishoole, the most important determinant of freshwater survival of salmon was the deleterious effect of hatchery fish in the spawning cohort for salmon. While stocking is seen by many as a possible management action to conserve and bolster stocks, evidence continues to mount that where a wild population is present, and habitat is available, stocking is misguided (McGinnity et al. 2009, Bacon et al. 2015). The impact of reduced marine survival as a result of sea lice parasitism (Poole et al. 1990, Gargan et al. 2006, Thorstad et al. 2015) on the Burrishoole migratory trout was very significant, and transformed the dynamics of the population. Any relationship with land use change was likely to pale into insignificance in comparison, and we found this to be the case. In the case of salmonids, direct anthropogenic impacts, which in hindsight could have been avoided or minimised, have posed the greatest risk to the conservation of stocks in Burrishoole, notwithstanding the significant influence of climatic factors. The lesson to be learned here must surely be to minimise those impacts that we now know are likely to affect stocks of diadromous fish, with the knowledge that there are many unpredictable and less easily controlled confounding effects on the horizon. Finally, the role that an ecosystem approach using long term ecological monitoring must play in providing the evidence needed to manage diadromous fish stocks cannot be underestimated.

Acknowledgements

The authors sincerely thank the many staff of the Marine Institute research station in Burrishoole who have maintained the migratory fish census over five decades. The Environmental Protection Agency in Ireland funded the project which supplied some of the data for this work (ILLUMINATE # 2005-W-MS-40). P. McGinnity was supported by the Beaufort Marine Research Award in Fish Population Genetics funded by the Irish Government under the Sea Change Programme. Marzena Olas, Kim Olaya-Bosch and Karin Sparber helped with the collection of the core data.

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

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

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

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

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

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

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

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

Figure legends

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

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

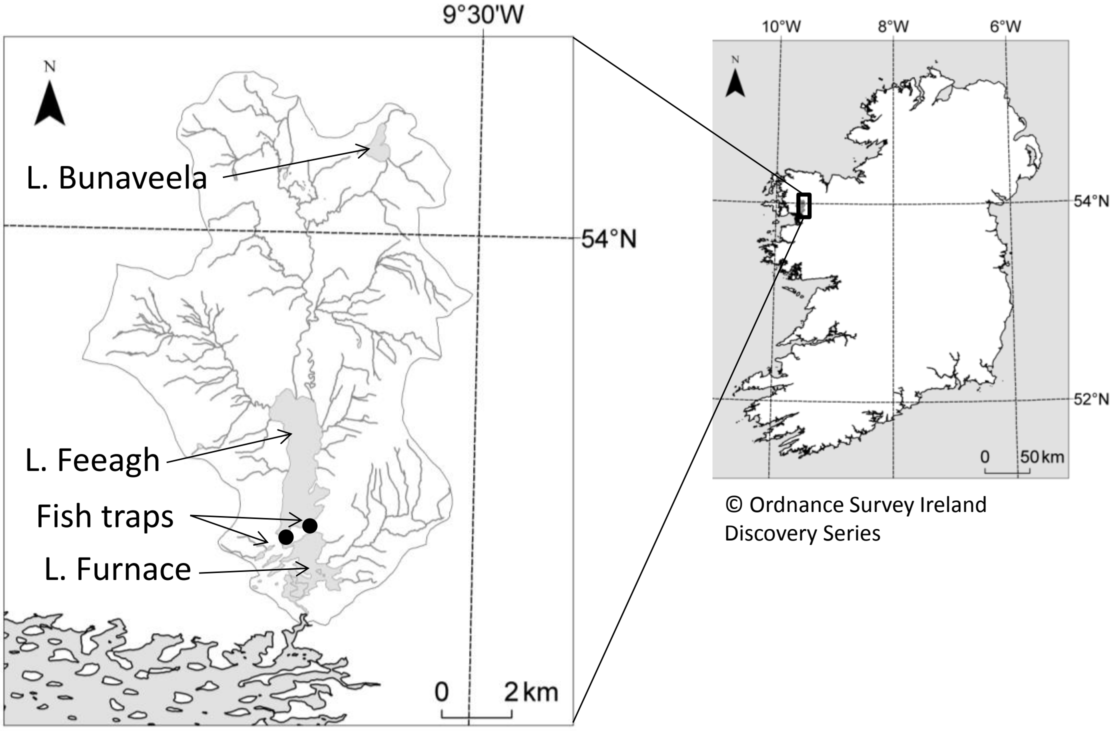
Fig. 3. Stock recruitment curves for salmon (left) and trout (right) from the Burrishoole catchment. Dotted lines indicate the best fit SR curve. For salmon: R^2= 89%, m=6352 (eq.1). For trout: R^2= 80%, a=18087, b=3.312 (eq. 2). See main text for equation details.

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

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

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

describing trout egg-smolt freshwater survival in the Burrishoole catchment between 1972 and 1989. The lines indicate mean model fit ± 95% c.i.’s in shaded polygons.



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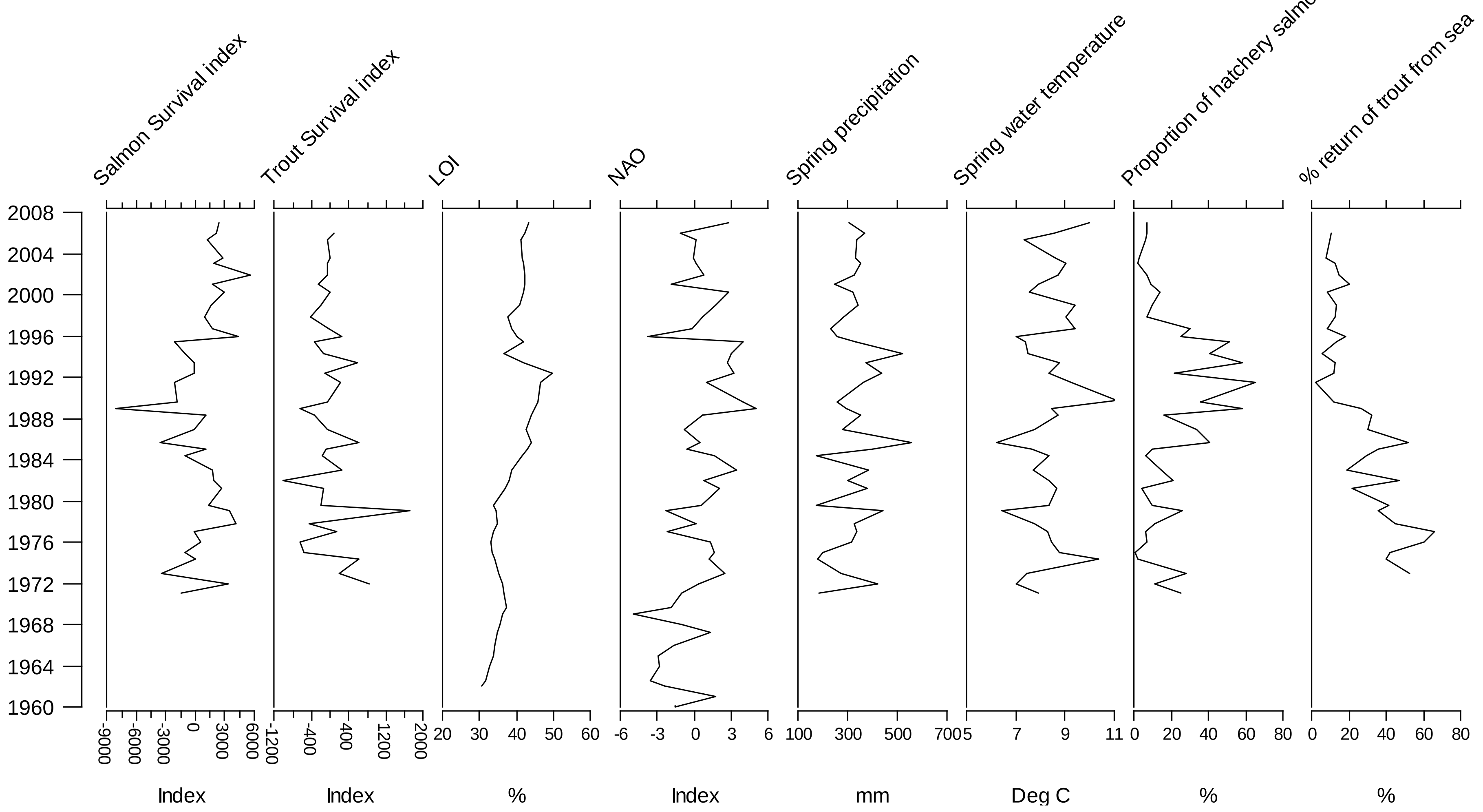
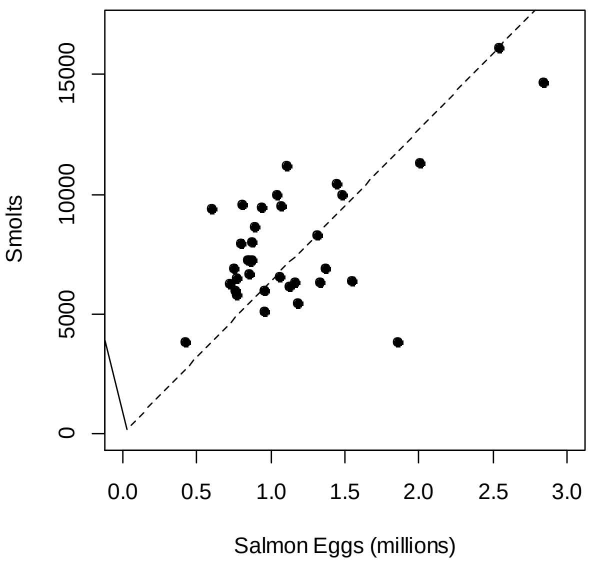
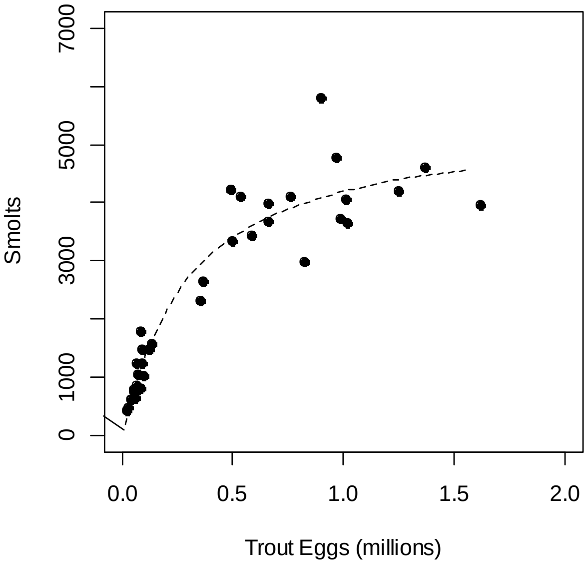

Salmon Survival index
Trout Survival index
LOI
NAO
Spring precipitation
Spring water temperature
Proportion of hatchery salmon
% return of trout from sea
2008
2004
2000
1996
1992
1988
1984
1980
1976
1972
1968
1964
1960
-9000
-6000
-3000
0
3000
6000
Index
-1200
-400
400
1200
2000
Index
20
30
40
50
60
%
-6
-3
0
3
6
Index
100
300
500
700
mm
5
7
9
11
Deg C
0
20
40
60
80
%
0
20
40
60
80
%


Smolts
0
5000
10000
15000
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Salmon Eggs (millions)


Smolts
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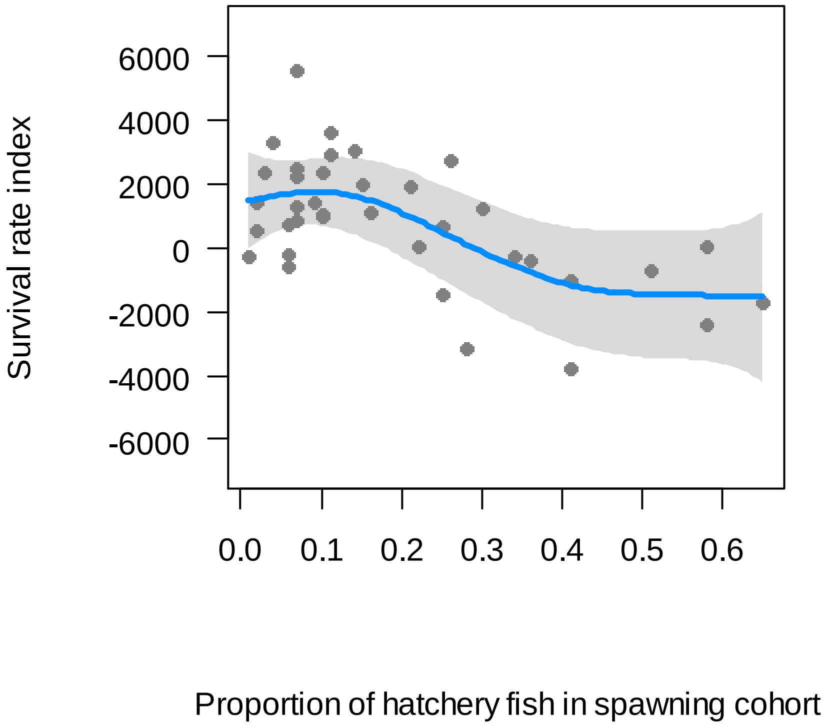
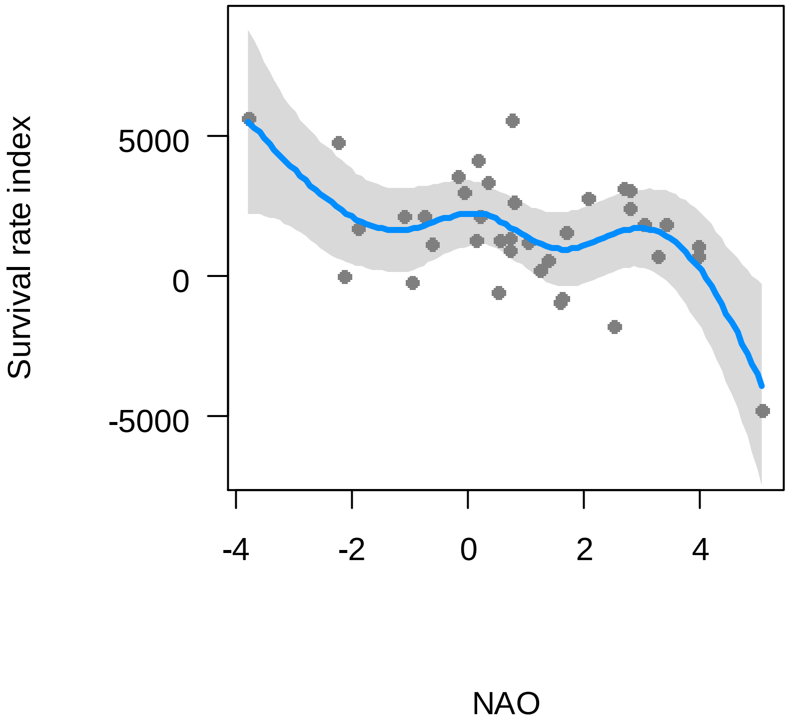
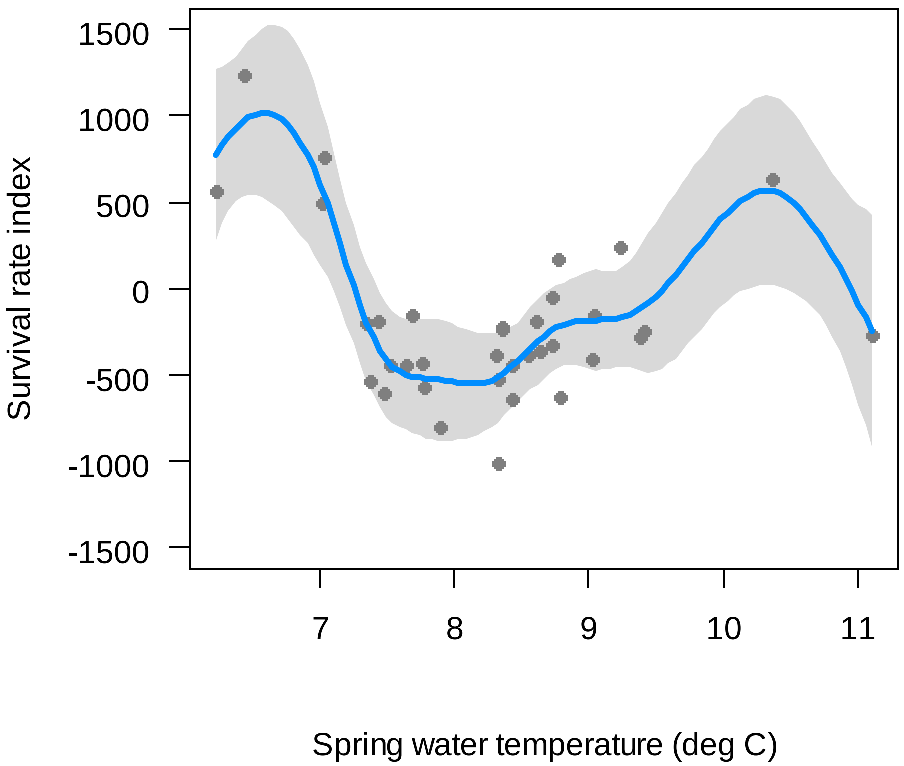
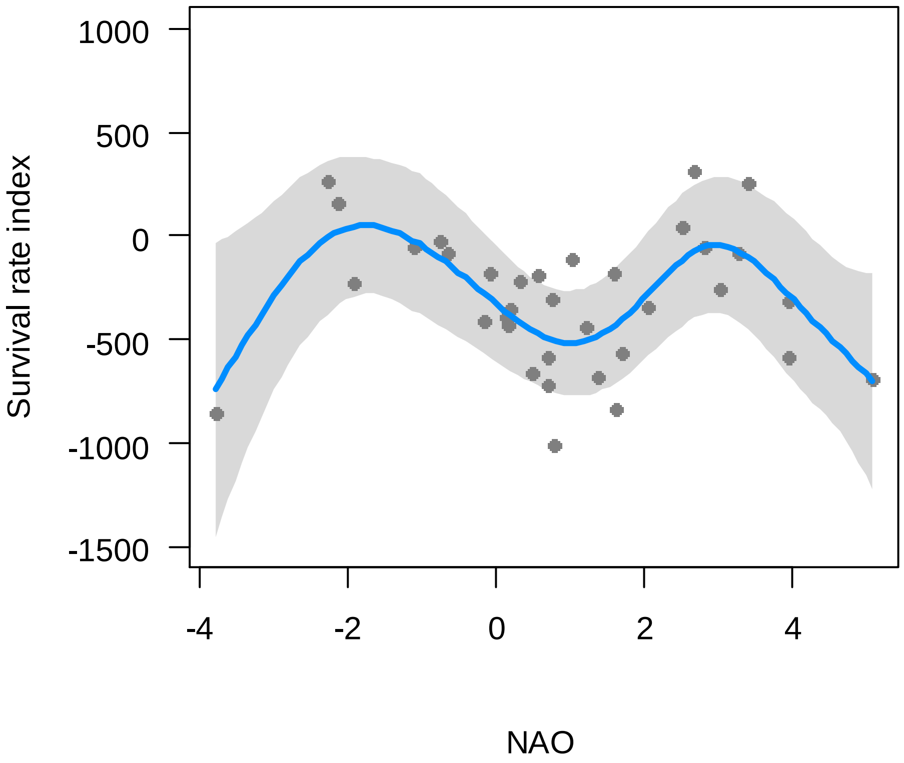
1000
3000
5000
7000
0.0
0.5
1.0
1.5
2.0
Trout Eggs (millions)


Survival rate index
6000
4000
2000
0
-2000
-4000
-6000
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Proportion of hatchery fish in spawning cohort


Survival rate index
5000
0
-5000
-4
-2
0
2
4
NAO


Survival rate index
1500
1000
500
0
-500
-1000
-1500
7
8
9
10
11
Spring water temperature (deg C)


Survival rate index
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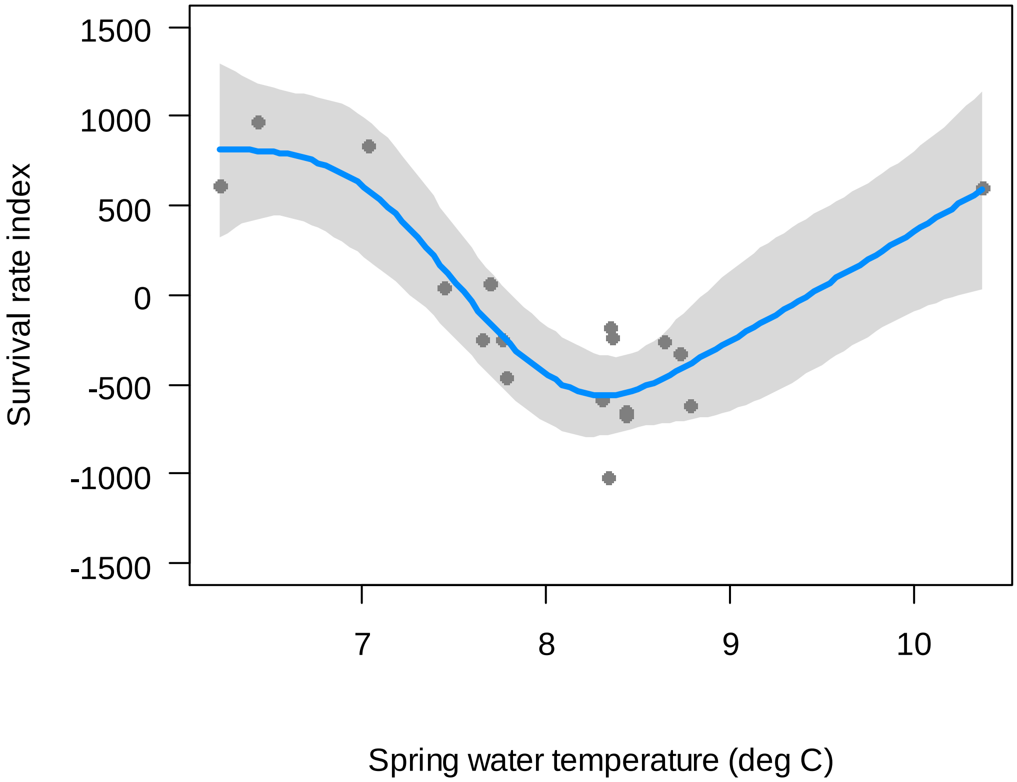
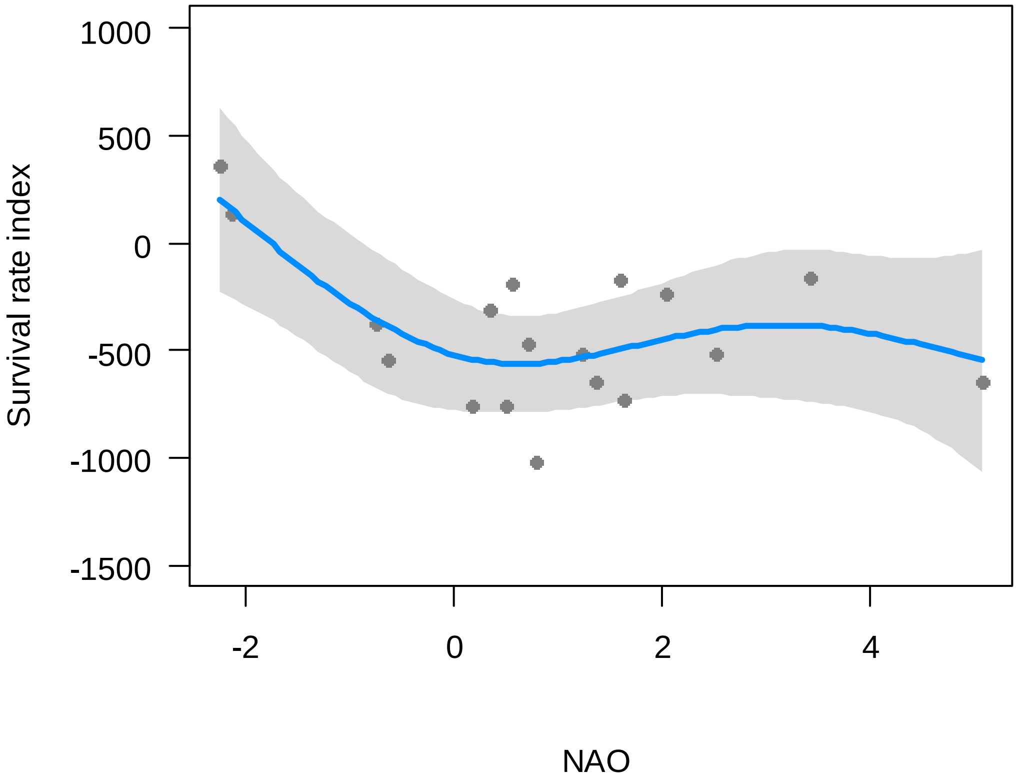
500
0
-500
-1000
-1500
-4
-2
0
2
4
NAO


Survival rate index
1500
1000
500
0
-500
-1000
-1500
7
8
9
10
Spring water temperature (deg C)


Survival rate index
1000
500
0
-500
-1000
-1500
-2
0
2
4
NAO