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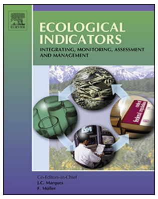

Original Articles

Development of a large-scale juvenile density model to inform the assessment and management of Atlantic salmon (*Salmo salar*) populations in Scotland

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ABSTRACT

Electrofishing data are commonly collected to assess the status of salmonid populations. However, their interpretation can be challenging without a benchmark measure of abundance against which they can be compared, leading some practitioners to question the value of these data. Juvenile density models that relate salmonid abundance to habitat characteristics offer one approach for developing spatially explicit benchmark abundances. This study collated and analysed an electrofishing dataset for Atlantic salmon (*Salmo salar*) collected across Scotland between 1997 and 2015. Habitat was characterised using landscape proxies, derived from large scale spatial datasets. A two stage modelling approach related (1) capture probability to landscape and other covariates (2) fish density to landscape and other covariates, having adjusted for differences in capture probability. Capture probability varied with monitoring organisation, year and region, responded modally to day of the year, and decreased with upstream catchment area, river distance to sea and gradient. Salmon density increased non-linearly with upstream catchment area and river distance to sea and decreased with the percentage of the riparian zone containing conifer trees. There was a south-north gradient in density, with higher densities in the north. The density model was used to develop benchmark salmon densities (reference conditions) that would be expected in river catchments that are relatively un-impacted by anthropogenic pressures and are associated with high spawner densities, resulting in near-saturation of available freshwater habitat. The benchmark densities were based on the fixed effects from the density model, excluding the effects of riparian conifer woodland and the south-north gradient, adjusted for the site-wise mean observed density in the dataset. Comparing catchment scale predictions of juvenile production against this benchmark (or some percentage of it) could provide a valuable assessment tool.

1. Introduction

Atlantic salmon (*Salmo salar*) is an anadromous species of high economic and conservation value that is widely distributed across North West Europe and North East America. The species is subject to international management agreements (North Atlantic Salmon Conservation Organisation, NASCO) and legislation (e.g. The European Commission Habitats Directive, 92/43 EEC) that aim to protect and maintain the species whilst balancing conservation needs with fisheries exploitation and economic development. Scotland contains 17 Special Areas of Conservation (SACs) for salmon under the European Commission Habitats Directive and Scottish salmon stocks account for ca. 75% and 30% of the UK and EU wild salmon production respectively (ICES, 2016). Recent estimates of the economic importance of salmon to Scotland suggest that recreational fisheries contribute ca. £79.9 million each year to the rural economy (PACEC, 2017). Management of this valuable resource therefore requires tools that provide objective assessments of the status of fish populations, the impact of environmental pressures and the outcome of management actions.

Juvenile assessment is a potential approach for determining the status of salmonid populations and informing management across a range of spatial scales, from river reach to catchment or region.

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Juvenile abundance is monitored by fisheries managers using methods such as electrofishing (Millar et al., 2016), trapping (Bryant and Woodsmith, 2009) and snorkelling (Steel et al., 2016) and is often the most extensive source of information on salmonids. Nevertheless, these data are frequently used by managers to illustrate population trends rather than status which is more challenging to determine. Status assessments require benchmark measures of abundance for comparison that describe the target density for locations of interest (Cowx and Fraser, 2000; Godfrey, 2005; Milner et al., 1998). Where benchmarks are intended to reflect near-natural conditions (i.e. un-impacted rivers), and healthy fish populations (spawner saturated habitats), they are often referred to as reference condition (Moss et al., 1987; Stoddard et al., 2006), habitat potential or intrinsic potential (Burnett et al., 2007). The development of defensible, spatially explicit benchmarks for fisheries management depends on the availability of suitable habitat - abundance models (Milner et al., 1998).

Atlantic salmon typically spend between one and three years in fresh water before migrating to sea as smolts. During this time their distribution and abundance is strongly influenced by habitat requirements, which vary with fish size, age and time of year (Armstrong et al., 2003; Millidine et al., 2016). During the spring and summer of their first year, fry (0 year old juveniles) typically reside in habitats with shallow fast moving water and gravel/cobble substrate close to parental spawning locations (Teichert et al., 2011). As they grow and enter their second year in freshwater, parr (≥1 year old salmon) disperse over greater distances and use a wider range of habitats, favouring areas with greater depths and velocities and coarse substrates that provide shelter from predators (Foldvik et al., 2017).

Traditional models of juvenile salmonid abundance derived from census data (e.g. electrofishing or snorkelling) have focussed on relationships between fish numbers and reach-scale channel characteristics observed at the time of sampling; e.g. depth, substrate or morphological unit (Baglinière and Champigneulle, 1986; Fausch et al., 1988; Milner et al., 1998). These descriptors are directly or indirectly indicative of underlying habitat requirements (e.g. depth, velocity, shelter, food provision). However, they often have limited explanatory power at larger spatial scales (Pépino et al., 2017) and in aggregated datasets are not always recorded consistently, if at all. Furthermore, field-based characterisation of habitat is often time consuming and only available for a small portion of the river network (Steel et al., 2016). This limits the ability of models to predict juvenile abundance at larger spatial scales or to estimate system (catchment) production by scaling up to whole river networks (Glover et al., 2018; Isaak et al., 2017). Additionally, local habitat characteristics can be susceptible to anthropogenic impacts so, whilst field observed habitat characteristics can be useful for predicting current fish abundance, they are less useful for predicting benchmark densities, unless the natural characteristics of the river can also be defined with confidence.

Recent studies have related measures of juvenile salmonid abundance to landscape characteristics (e.g. altitude, upstream catchment area) derived remotely from spatial datasets such as digital elevation models, digital river networks and landuse datasets (Bryant and Woodsmith, 2009; Foldvik et al., 2017; Milner et al., 1998; Pépino et al., 2017; Steel et al., 2016; Thompson and Lee, 2000). These landscape characteristics operate as proxies for the geomorphological, hydrological and hydraulic processes that control habitat quality (Foldvik et al., 2017; Steel et al., 2016) and thus provide a basis for predicting salmonid densities at large spatial scales where field-based characterisation of habitat is not possible. Predictions based on landscape characteristics might also be used to establish benchmark densities against which juvenile census data could be compared to establish the status of sites, stocks, rivers or regions.

Despite the potential utility of landscape – juvenile abundance models as assessment tools, their development at large spatial scales is technically challenging because (1) automated approaches are required to describe landscape characteristics across many sites (2) the probability of capture in electrofishing data (or observation in snorkelling data) can vary with the same landscape characteristics that influence abundance (Glover et al., 2018; Millar et al., 2016) (3) abundance and capture probability are often spatially correlated at regional levels (4) juvenile census data are often unbalanced spatially and temporally (5) complex random effects structures can be required to characterise variation between catchments, sites, sampling events and years and to allow for correlation between life-stages (6) relationships between habitat, capture probability and abundance can have a range of nonlinear forms (e.g. asymptotic, modal).

This paper develops a national juvenile salmon density model for Scotland that addresses these technical challenges and that can be used to inform future assessments of the status of Scotland's salmon stocks. It builds on the work of Millar et al. (2016) who developed a framework for modelling capture probability and applied the techniques to Scotland-wide data, and Glover et al. (2018) who showed how the capture probability estimates could then be incorporated in a density model, in their case for a small catchment. The objectives of the paper are to (1) characterise spatial variability in habitat across Scotland using landscape covariates generated remotely from spatial data (2) model spatio-temporal variability in capture probability in relation to landscape covariates, location, time, life-stage and data collection organisation (3) model spatio-temporal variability in juvenile salmon density in relation to landscape covariates, location and time, incorporating the estimates of capture probability (4) consider approaches for deriving benchmark densities to assess the status of salmon populations across Scotland.

2. Materials and methods

2.1. Study Site

Scotland covers an area of ca. 80000 km^2 with an altitudinal range of 0–1334 m. Rainfall totals vary between < 700 mm in eastern Scotland to > 4000 mm in the western highlands. Scotland's geology, topography and steep climate gradients have resulted in many rivers with highly variable characteristics (Anon, 2009; Soulsby et al., 2009). There are > 16000 individual river catchments draining to the sea, of which 255 have an area > 25 km^2. Catchments vary from < 1 km^2 to 5260 km^2 for the River Tay which has a mean annual discharge of ca. 5.3 km^3 (Soulsby et al., 2009). There are ca. 389 Scottish rivers in the NASCO salmon rivers database (Anon, 2009), 17 of which are Special Areas of Conservation (SAC) for Atlantic salmon under the EU Habitats Directive (Anon, 2009). Major population centres and industrial activity are focussed around the "central belt", the narrow area to the south of Scotland, and along the east coast (Fig. 1).

2.2. Electrofishing data

Three-pass depletion electrofishing data meeting the minimum requirements of the Scottish Fisheries Coordination Centre (SFCC) standards for fully quantitative sampling (Scottish Fisheries Co-ordination Centre, 2007) were collated from 25 organisations consisting of local fisheries trusts, District Salmon Fisheries Boards, Marine Scotland Science (MSS) and the Scottish Environment Protection Agency (SEPA). Data from local trusts and Boards were generally constrained to their geographic area of responsibility, except where carrying out work under contract or for national purposes such as assessing the status of SACs. MSS and SEPA have a national remit and thus sample more widely, but at fewer sites. The collated data were not based on an overarching sample design, but were collected for a variety of research and assessment purposes relevant to the contributing organisations.

Before the widespread establishment of fisheries trusts, the electrofishing data were strongly biased to the east of Scotland, particularly the south east (Tweed catchment). The dataset was therefore restricted to the years 1997–2015 when there was greater spatial balance (Fig. 1). Sites above impassable barriers, where the whole river width was not