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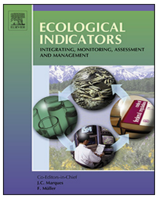

Original Articles

Incorporating estimates of capture probability and river network covariance in novel habitat – abundance models: Assessing the effects of conservation stocking on catchment-scale production of juvenile Atlantic salmon (*Salmo salar*) from a long-term electrofishing dataset

Ross S. Glover[a,b,*], Robert J. Fryer[c], Chris Soulsby[b], Philip J. Bacon[a], Iain A. Malcolm[a]

[a] *Marine Scotland Science, Freshwater Fisheries Laboratory, Faskally, Pitlochry PH16 5LB, Scotland, United Kingdom*
[b] *Northern Rivers Institute, School of Geosciences, University of Aberdeen, St. Mary's, Elphinstone Road, Aberdeen AB24 3UF, Scotland, United Kingdom*
[c] *Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB, Scotland, United Kingdom*

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ABSTRACT

There are increasing calls for "conservation stocking" to counter declines in Atlantic salmon (*Salmo salar*) populations, the assumption being that stocking can bypass population bottlenecks and increase recruitment over natural processes. However, there are too few quantitative studies with sufficient data to assess the efficacy of conservation stocking. The Girnock Burn is a unique long-term monitoring site where adult and juvenile salmon numbers have been monitored for over 50 years, including 11 years with conservation stocking. Adults were monitored at a fixed trap and juveniles were monitored by electrofishing. In stocked years, ova were incubated in surface water to reduce density-independent over-winter mortality. In eight years, eyed ova were stocked at uniform densities to reduce local density-dependence. In three years, stocking replicated natural spatial variability in ova deposition removing any potential benefits of reduced local density-dependence. Juvenile production was estimated by summing the product of reach-scale density estimates and river area obtained from a novel spatial statistical river network model that incorporated the effects of capture probability, habitat and stock level. Capture probability varied with life-stage (age 0+ fry or ≥1+ parr), electrofishing pass and day of the year, but importantly also exhibited a positive temporal trend across years. Survival from ova to fry was density-independent and higher under uniform stocking than natural spawning or simulated natural spawning. Under uniform stocking, fry densities varied smoothly with altitude, while under natural spawning and simulated natural spawning, fry exhibited a more patchy distribution. Increased fry production did not translate to increased parr production, which was strongly density-dependent. This likely reflected the inability of fry to move between stocked locations and suitable overwintering habitat, decreasing survival between fry and parr life-stages. Consequently, there was no overall benefit of stocking. The modelling framework used in this study provides a valuable approach for interpreting long-term datasets where site locations, equipment and staffing vary over time. The long-term Girnock dataset was valuable in separating management action from natural population regulation and permitting understanding of ecological processes. The study indicates that conservation stocking can be ineffective, even where implemented to best scientific standards. It is therefore recommended that a detailed understanding of local population dynamics is obtained, and a realistic appraisal of the expected benefits of stocking is undertaken, before management actions are considered.

1. Introduction

Stocking is widely applied in freshwater fisheries management to address objectives ranging from enhancement of fisheries to the preservation of threatened fish populations (Aprahamian et al., 2004; Cowx, 1994). Stocking has often been driven by long-term (decadal) declines in natural fish populations (Brunsdon et al., 2017; Molony et al., 2003) in response to anthropogenic pressures including overfishing, habitat degradation, habitat loss and impacts to river network connectivity. Stocking aims to maintain or increase fish production by

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* Corresponding author.
E-mail addresses: r.glover@marlab.ac.uk (R.S. Glover), r.fryer@marlab.ac.uk (R.J. Fryer), c.soulsby@abdn.ac.uk (C. Soulsby), p.bacon@marlab.ac.uk (P.J. Bacon), i.malcolm@marlab.ac.uk (I.A. Malcolm).

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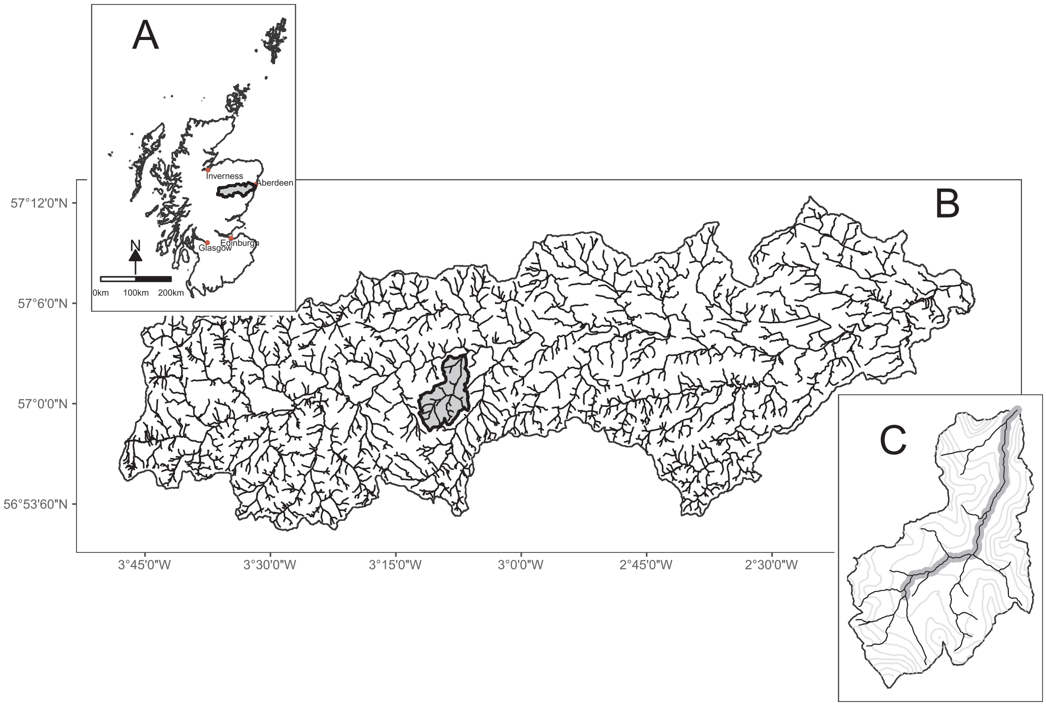

Fig. 1. (A) Map showing the River Dee within Scotland, (B) the Girnock Burn catchment (grey) within the River Dee catchment, (C) the Girnock Burn catchment with the shaded stream area showing the extent of ova stocking.

bypassing population bottlenecks and minimising mortality (Aprahamian et al., 2004; Roni et al., 2016; Waples et al., 2007). Where populations are substantially below carrying capacity, conservation (or restoration) stocking has been advocated as an approach to halt further reductions and preserve natural fish stocks (Aprahamian et al., 2003; Bacon et al., 2015).

Atlantic salmon (*Salmo salar*) is an anadromous species of high economic and conservation value that is frequently the focus of management action across Europe and North America. In recent decades, reductions in marine survival (Chaput, 2012; Kennedy et al., 2012), compounded by habitat loss and degradation have led to sharp declines in returning adult numbers across much of their geographic range (Mills et al., 2013; Parrish et al., 1998) prompting many conservation programmes (Griffiths et al., 2011; Jonsson and Jonsson, 2009). In Scotland, early-running multi-sea-winter “spring” salmon have declined faster than other stock components (Youngson et al., 2002) giving particular concern over their status. This has resulted in a cessation of commercial fishing and the introduction of compulsory catch and release for sport fisheries during the spring. However, it has also renewed calls for conservation stocking programmes to be established on affected rivers. In contrast to enhancement stocking which aims to improve local fisheries by supplementing natural stocks with hatchery fish (Naish et al., 2007), conservation stocking focusses on maintaining freshwater production (Bacon et al., 2015) while preserving genetic integrity and fitness of progeny and avoiding introductions (Trushenski et al., 2015). While the objectives of conservation stocking are clear, the efficacy of such programmes remains contentious. Conclusions are often hampered by a reliance on potentially spurious correlations between stocking and indicators of abundance (e.g. adult salmon returns; Bacon et al., 2015; Naish et al., 2007) exacerbated by the timing of management action, e.g. conservation stocking is often triggered at critically low levels with any subsequent population increase attributed to stocking. The inability to separate natural population regulation (inter and intra-cohort competition) from stocking effects (Aprahamian et al., 2003; Bacon et al., 2015; Waples et al., 2007) and insufficiently detailed process understanding at relevant spatial and temporal scales also make it hard to establish the circumstances under which stocking is effective.

Although conservation stocking programmes assume that hatcheries and stocking can bypass high mortality during early life-stages (e.g. egg to fry or fry to parr), their success is often assessed (if at all) at migratory life history stages (emigrating smolts or returning adults) where enumeration of system production can be more straightforward. Estimation of production at earlier life-stages (fry or parr) requires upscaling from multiple reach-scale estimates of fish density (electrofishing or snorkelling sites) to the network scale. This can be technically challenging in the case of electrofishing removal methods because accurate density estimation relies on adequate characterisation of capture probability, which can vary with habitat, season, equipment, staff and protocols (Millar et al., 2016), and because fish abundance tends to be spatially correlated at fine spatial scales (Isaak et al., 2017).

This study investigates the effect of conservation stocking on juvenile Atlantic salmon production in the Girnock Burn, an upland spring salmon tributary of the Aberdeenshire River Dee, Northeast Scotland, using a dataset collected over 50 years, including 39 years of juvenile data. It builds on a previous investigation by Bacon et al. (2015) that found conservation stocking did not increase emigrant production from a fixed spawner resource, despite well documented effects of patchy spawning habitat (Moir et al., 1998; Webb et al., 2001b) and poor ova survival (Malcolm et al., 2005) which would be expected to constrain natural production. In particular, this paper aims to identify the life-stages and mechanisms that constrained the expected benefits of stocking. Recent advances in capture probability models (Millar et al., 2016) and spatial statistical river network modelling (Jackson et al., 2017; O’Donnell et al., 2014) are combined to estimate production from a juvenile habitat model that accounts for potential sources of bias and gives valid estimates of precision. The effects of stocking are assessed by comparing production in years of natural spawning and stocking, having accounted for temporal variability in ova deposition. The specific objectives of the study are: (1) obtain accurate estimates of fish density from electrofishing data (2) fit a spatio-temporal juvenile habitat density model that incorporates the effects of stock level (ova deposition) and stocking (3) illustrate the effect of stocking on the spatial distribution of salmon fry and parr (4) assess the influence of ova stocking on salmon production to the fry and parr life-stages at the