Long-Term Recruitment Patterns of 0+ Brown Trout in the River Maine, Northern Ireland

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Abstract Lough Neagh is the largest freshwater lake in the UK and Ireland (392 km^2) and has a stock of lake migrating brown trout which recruit/spawn in the influent tributaries and mature in the lake. Potamodromous trout are exploited commercially in Lough Neagh with total landings ranging from c. 0.3 to 29.4 tons year^{-1} between 2001 and 2020. The recruitment of 0+ trout has been assessed annually on the River Maine, a large tributary of Lough Neagh, across an extensive and consistent network of Semi-Quantitative electric fishing sites between 2002 and 2020. The annual trout recruitment index for the River Maine was analysed against a range of potential explanatory variables including estimates of adult trout migration into the river, the commercial landings from the lake, electric fishing indices of Atlantic salmon (*Salmo salar* L.) recruitment and various discharge metrics. A stock–recruitment relationship was evident between the run of adult trout measured through the River Maine fish counter and subsequent 0+ recruitment measured in the following year.

Keywords Discharge, Potamodromy · Stock–recruitment · *Salmo trutta*

1 Introduction

Stream dwelling brown trout, *Salmo trutta* L., can display marked diversity in morphology and life history (Ferguson et al. 2017) with up to five different life history-migratory strategies possible (Ferguson et al. 2019). Some *S. trutta* stocks are characterised by a potamodromous life history strategy in which lacustrine–adfluvial movements may occur involving migrations between a lake and an influent river (Northcote 1997). The freshwater environment in Northern Ireland is

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dominated by two large lake catchments, Lough Neagh (surface area 396 km^2) and Lower Lough Erne (surface area 109 km^2). The influent streams on these lake systems support extensive stocks of potamodromous trout which in turn sustain important recreational fisheries across both catchments and a significant commercial fishery in Lough Neagh (Kennedy et al. 2021). The River Maine is a major tributary of Lough Neagh and is noted for its strain of lake running brown trout, known locally as dollaghan trout. A fishery monitoring programme was initiated in the River Maine in 2001–02 with a routine, semi-quantitative (SQ) electric fishing survey (Crozier and Kennedy 1994) conducted annually at 199 sites throughout the range of migratory salmonids across the river (Kennedy et al. 2014). A fish counter was also commissioned on the lower river in 2001 to provide an assessment of adult spawning runs.

The recruitment success of 0+ salmonids is influenced by a diverse range of biological and environmental parameters that may function in synergy (Imre et al. 2002; Armstrong et al. 2003). Milner et al. (2003) further outlined that juvenile trout abundance in streams can be regulated by density-dependent mechanisms (e.g. territorial competition) and/or density-independent factors (e.g. climate). Elliott (1989), for example demonstrated that population size in an anadromous *S. trutta* stock in the English lake district was regulated by density-dependent mortality operating over a relatively short critical period (c. 30–70 days) following the emergence of fry from the redds. The importance of density-independent factors has also been clearly illustrated for other stream dwelling brown trout stocks, with high flows during emergence significantly limiting subsequent 0+ densities in French rivers (Cattanéo et al. 2002).

The current study tabulated the long-term electric fishing data from the River Maine for the period 2002–2020, documenting and describing annual variations in recruitment of 0+ trout in the catchment. This enabled an investigation of relationships between the annual 0+ trout recruitment index and a panel of available explanatory biological and environmental variables, to define potential factors regulating recruitment.

2 Materials and Methods

2.1 Study Area

The River Maine is 45 km in length, has a catchment area of >200 km^2, average daily discharge of c. 24 m^3/s and flows into the northeast section of Lough Neagh in Northern Ireland (Fig. 1). The River Maine has three major tributaries including the Kellswater, Braid and Cloghwater and hosts a number of local angling clubs which mainly target the migratory 'dollaghan' brown trout. The other fish fauna common in the River Maine includes Atlantic salmon, *Salmo salar* L., eel, *Anguilla anguilla* L., minnow, *Phoxinus phoxinus* L., stickleback, *Gasterosteus aculeatus L.* and

Fig. 1 Location of River Maine catchment in Northern Ireland and insert showing distribution of individual electric fishing sites (black dots)

Stoneloach, *Barbatula barbatula L.* The River Maine catchment has a predominately agricultural (pastoral) land use, the underlying geology is granite and the river was subject to a historical arterial drainage scheme in the 1970s (Essery and Wilcock 1990).

2.2 Monitoring Data

Juvenile salmonids were monitored on the River Maine by a semi-quantitative (SQ) electric fishing programme, conducted across a standard network of 199 sites over a 19-year period (2002–2020). SQ survey sites were typically undertaken in shallow (<30 cm) nursery habitats, with a site located every 500–1000 m of channel length throughout all the tributaries and the main channel of the river. The survey design ensured complete coverage of the catchment and included all areas accessible to migratory fish (Kennedy et al. 2014). The SQ surveys were undertaken during the high summer (15th July–15th September) with the same locations, equipment and as far as possible the same survey staff used each year. The SQ sampling is a Catch-Per-Unit-Effort technique and involves electrofishing each site for a fixed time of 5 min using a single anode, portable backpack electrofishing apparatus and a single catcher (Crozier and Kennedy 1994). The SQ technique was designed specifically for 0+ salmonids and relies on standardisation of effort and high capture efficiency. Any ‘missed’ fish that are observed to evade the catcher are noted and any site where capture efficiency drops below 60% is discarded and re-visited at a later date (Crozier and Kennedy 1994). All fish caught during the survey were anaesthetised using Tricaine methanesulphonate (MS-222), identified and measured for fork length L_F (mm) before being returned alive to the river. A subsample of fish had scale samples removed for age determination and salmonid species were split between 0+ and >0+ age classes according to L_F. The catch data for each site was expressed as a catch-per-unit-effort (CPUE) index detailing the number of fish (by species and age class) captured per 5 min (e.g. number 0+ trout/5 min). The SQ electric fishing survey data were tabulated each year with the catchment divided into 18 geographically sequenced sections (Table 1). The mean CPUE index for 0+ trout was calculated for each section and then the overall catchment-scale recruitment index was determined as the mean of the 18 sections (Table 1).

Upstream migrant salmon and trout in the River Maine are monitored using an Aquantic (™) 2100C resistivity fish counter, installed into the fish pass at a weir situated c. 3 km from the confluence with the lake. The weir feeds an adjacent hydroelectric side channel which diverts a portion of the river flow and ensures that the fish pass is the main upstream passage route for migratory trout ascending the river. The counter is known to detect a number of Atlantic salmon which are larger than the migratory trout and contribute to the total upstream count each year. Calibration work was undertaken at the fish counter site using CCTV imaging, direct sampling and length frequency analysis to differentiate between upstream trout and salmon movements. Trout were observed to consistently compose the bulk

Table 1 Example of semi-quantitative electric fishing survey results for 0+ age class trout collected from the River Maine in 2011

Sub-catchment	Sub-catchment section	E-Fishing survey site nos.	No. sites completed (2011)	CPUE (no 0+ /5 min)
Kellswater	Kells Top	1–14	14	8.29
Kellswater	Kells Upper	15–22	8	7.75
Kellswater	Kells Middle	23–33	7	5.22
Kellswater	Kells Bottom	34–47	5	3.00
Kellswater	Kells Minor Tribs	10	10	9.78
Braid	Braid Upper	1–11	11	8.36
Braid	Braid Middle	12–24	13	5.17
Braid	Braid Bottom	25–35	11	2.60
Braid	Braid Minor Tribs	16	12	5.73
Clough	Clough Upper	1–10	10	4.30
Clough	Clough Middle	11–20	10	3.90
Clough	Clough Bottom	21–31	11	5.67
Clough	Clough Tribs	10	10	5.20
Cloughmills	Cloghmills Upper	1–8	8	8.83
Cloughmills	Cloghmills Lower	9–17	9	4.57
Killagan	Killagan	1–13	2	4.55
Maine	Main 1	1–12	4	5.00
Maine	Main 2	13–20	8	2.67
Total sites surveyed 2011			163	
Mean catchment CPUE index (no. 5 min^{-1})				*5.59*

of the count (>90%) and a size threshold was established for application to the counter detections to separate the annual salmon count. The counter has been operational on the river since 2001. A flow gauging station is also available on the River Maine close to the fish counter site at Randalstown and the mean daily river discharge (m^3/s) was tabulated for the period 2000–2020.

2.3 Analysis

Annual 0+ trout recruitment indices were investigated against a panel of potential explanatory biological and environmental time series. Explanatory biological variables included estimates of adult abundance from the previous year represented by the adult trout count (yr^{-1}) and the total commercial catch of dollaghan from Lough Neagh (yr^{-1}). Additional parameters considered included electric fishing derived SQ indices of >0+ trout parr and 0+ salmon abundance in the same year (yr). Discharge data measured at the flow gauging station on the River Maine were also considered and mean daily flow records were tabulated to determine Mean Monthly Flow (MMF), mean flow during the adult migratory season (Aug–Oct) and mean flow over the ova to fry development phase (Nov–Apr) prior to each 0+ monitoring year. The number of high flood events (>Q 1 flows) that occurred during the development of each 0+ cohort (previous Nov–Apr) were also considered as a potential explanatory variable.

The individual time series were assessed for autocorrelation. Each time series, with the exception of the trout parr index, were stationary. Applying first-order differencing to the >0+ trout parr index time series induced stationarity. A cross-correlation analysis was conducted to investigate the potential association between the various input time series, which for the >0+ trout parr index was the first-ordered differenced time series, and the output time series which was 0+ juvenile trout recruitment. All time series analyses were conducted using R (R Core Team 2021).

Emergence of 0+ trout from spawning redds typically occurs sometime between early April to mid-May across the River Maine. The impact of discharge on recruitment was investigated specifically at this critical time and the 0+ recruitment index was compared against the river discharge in April and May earlier that year.

In order to consider the role of density dependence on the River Maine stock the annual 0+ trout recruitment indices were modelled against the adult fish count from the previous year (yr^{-1}) to explore any possible relationship between stock (fish counter estimates) and recruitment (SQ 0+ indices). Two classic stock–recruitment models were applied to the dataset including the Ricker model (Ricker 1954);

$$R = a\,\mathrm{S}\exp^{-b\mathrm{S}}$$

where S = Breeding stock [count yr^{-1}], R = recruitment [SQ index yr], a and b are constants. Secondly the Beverton-Holt model was applied (Beverton and Holt 1957);

$$R = a^* S / \left(1 + b^* s\right),$$

where S = Breeding stock [count yr^{-1}], R = recruitment [SQ index yr], a and b are constants.

Each stock–recruitment model was tested against an alternative density-independent model describing the mean recruitment values for the dataset. The Akaike Information Criterion (AIC) and the extra sum-of-squares test were used to compare the respective S–R model against the density-independent model. The amount of variation explained by each non-linear model was calculated as the pseudo-r^2, that is the correlation between the observed and fitted values squared. The analyses were conducted using *R* (packages FSA, dplyr, magrittr, plotrix, nlstools, lsmeans, magrittr, nlstools plotrix and qpcR).

3 Results

The juvenile (0+) trout recruitment index for the River Maine, monitored by the SQ survey programme and expressed as a relative abundance index (mean no. 0+ trout 5 min^{-1}), has varied from 5.6 (2011) – 14.7 0+ trout 5 min^{-1} (2020) across the time series (Fig. 2). The mean relative abundance was 10.5 0+ trout 5 min^{-1} and the coefficient of variation was 3.3 indicative of fair variation across the available time series. Older trout parr (>0+) were less abundant in the surveys and ranged from 1.3

Fig. 2 Mean annual abundance indices (no. fish/5mins) for 0+ and >0+ brown trout, developed from semi-quantitative electric fishing surveys across the River Maine catchment between 2002 and 2020

(2010) – 3.7 > 0+ trout 5 min^{-1} (2019) (Fig. 2) with a mean level of 2.4 > 0+ 5 min^{-1} and showed a lower coefficient of variation of 2.9.

The abundance of returning adult trout, as quantified by the resistivity fish counter on the Lower River Maine, varied markedly from 390 (2010) to 4461 (2018) (Fig. 3). Landings of dollaghan trout from the commercial fishery in Lough Neagh, included fish originating from all the influent lake tributaries including the Maine, were also highly variable across the time series and catch returns varied from 334 kg (2004) to 29,441 kg (2015) (Fig. 3).

Prior to cross-correlation analysis the response and explanatory time series' were assessed for autocorrelation. Each of the time series, with the exception of the >0+ trout parr index dataset, was stationary. Applying first-order differencing to the >0+ trout parr index time series induced stationarity. A significant positive cross-correlation was observed between the 0+ trout recruitment index time series and the salmon fry index ($r = 0.68$). No other significant relationship was evident although weak positive correlations were evident between the 0+ trout recruitment index and both the adult count and commercial landings from Lough Neagh from the previous season (Fig. 4). Spring discharge on the River Maine, co-incident with 0+ trout emergence, has varied extensively across the time series with mean April flows ranging from 5.1 m^3/s (2020) to 24.0 m^3/s (2009) and mean May flows ranging from 2.7 m^3/s (2020) to 22.8 m^3/s (2012) (Fig. 5). The mean 0+ trout recruitment index was explored against river discharge levels in April and May and no linear, parabolic or polynomial relationships were evident (Fig. 6).

The 0+ trout recruitment index was further investigated for possible density-dependent relationships against a measure of adult trout abundance (fish counter) from the previous year. The Beverton-Holt model provided an improvement over the density-independent model (extra sum-of-squares test, sum of squares =5.38,

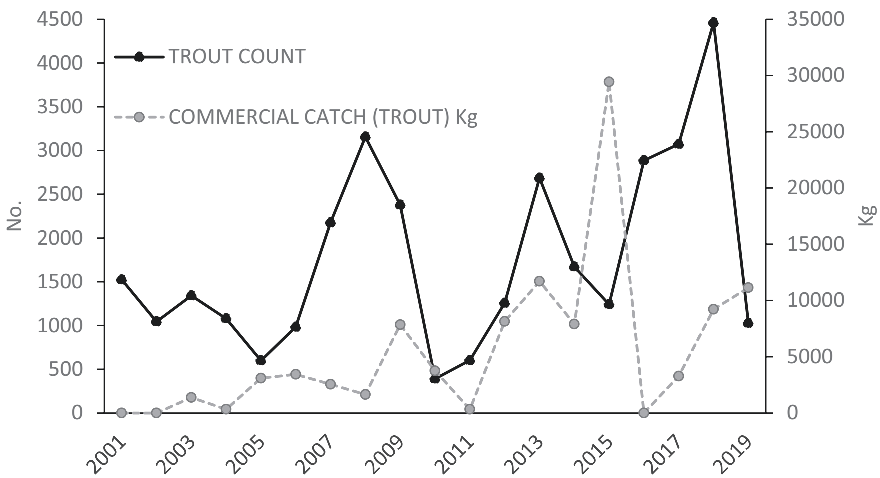

Fig. 3 Annual count of dollaghan trout from the River Maine resistivity fish counter and the total commercial landings of trout from Lough Neagh 2001–2019

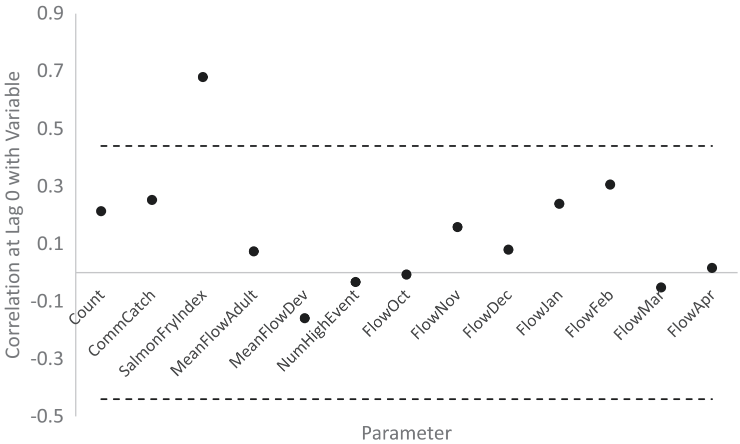

Fig. 4 Cross-correlation analysis of 0+ trout recruitment index against a panel of potential influential biological and environmental variables. Note; MeanFlowAdult = Mean discharge over the period August–October; MeanFlowDev = Mean discharge over the period November–April. The 95% confidence intervals are indicated by dashed lines

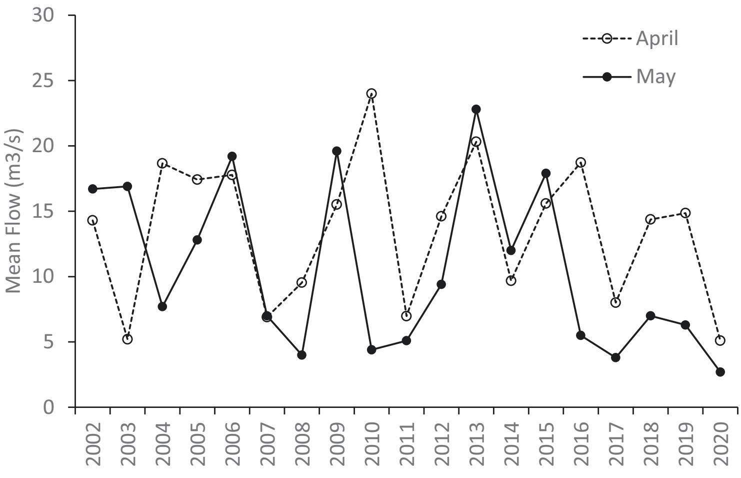

Fig. 5 The mean discharge (m^3/s) for April and May, measured at the River Maine gauging station, 2002–2020

$F_{(1, 17)} = 67.89$, $P < 0.001$). The Akaike Information Criterion (AIC) for the density-independent and Beverton-Holt density-dependent models were 38.18 and 9.63, respectively.

The Ricker model also provided an improvement over the density-independent model (extra sum-of-square test, sum of squares = 5.30, $F_{(1, 17)} = 63.22$, $P < 0.001$). Comparing the AIC for both models, which were 38.18 and 10.71 for the density-independent and for Ricker models, respectively, further confirmed the Ricker

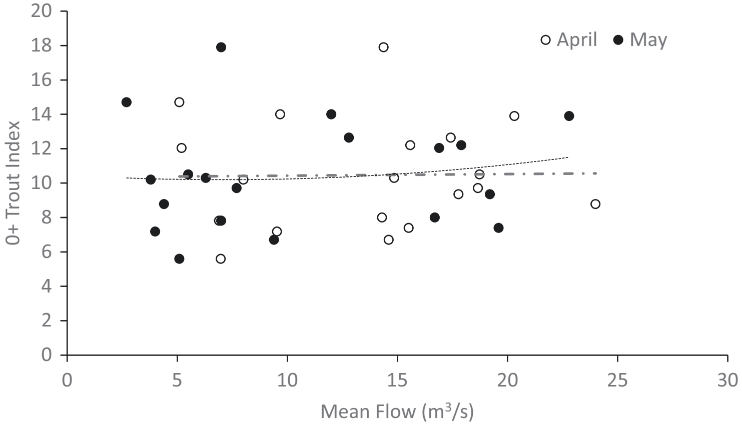

Fig. 6 0+ trout recruitment index plotted against mean monthly discharge in the preceding spring (April, May) across the monitoring period 2002–2020

model was an improvement over the density-independent model. The Akaike weights were 0, 0.37 and 0.63 for the density-independent, Ricker and Beverton-Holt models, respectively. The relative likelihood of the density-independent model was zero times and the Ricker model was 0.58 times as probable as the Beverton-Holt model to minimise information loss. The Beverton-Holt exhibited a pseud-r^2 value of 0.14 and the model constants were $a = 42.2$; $b = 3.4$ (Fig. 7a). The Ricker model had a pseudo-r^2 value of 0.13, parameters were $a = 17.3$; $b = 0.5$, and it indicated that the adult spawning stock (S_M) that yielded maximum recruitment was 1996 fish whilst the stock level that provided the maximum surplus production (S_G) was 1721 fish (Fig. 7b).

4 Discussion

Recruitment is the fundamental determinant of brown trout year-class strength and the identification of significant recruitment drivers represents a major research goal in fisheries science (Lobón-Cerviá et al. 2017). The influence of density-independent and density-dependent processes in 0+ trout recruitment has been investigated, compared and debated across a range of European case studies (Nicola et al. 2008; Lobón-Cerviá et al. 2017). Grant and Imre (2005) postulated that the regulation of stream dwelling salmonid populations was primarily driven by mortality and emigration at higher densities through interference competition, and by density-dependent growth via exploitative competition for food at lower densities. The impact of density dependence on individual growth is particularly important and has been well documented in a number of previous studies (Bohlin et al. 2002; Lobón-Cerviá 2005). Grossman and Simon (2020) reviewed 199 datasets across 21

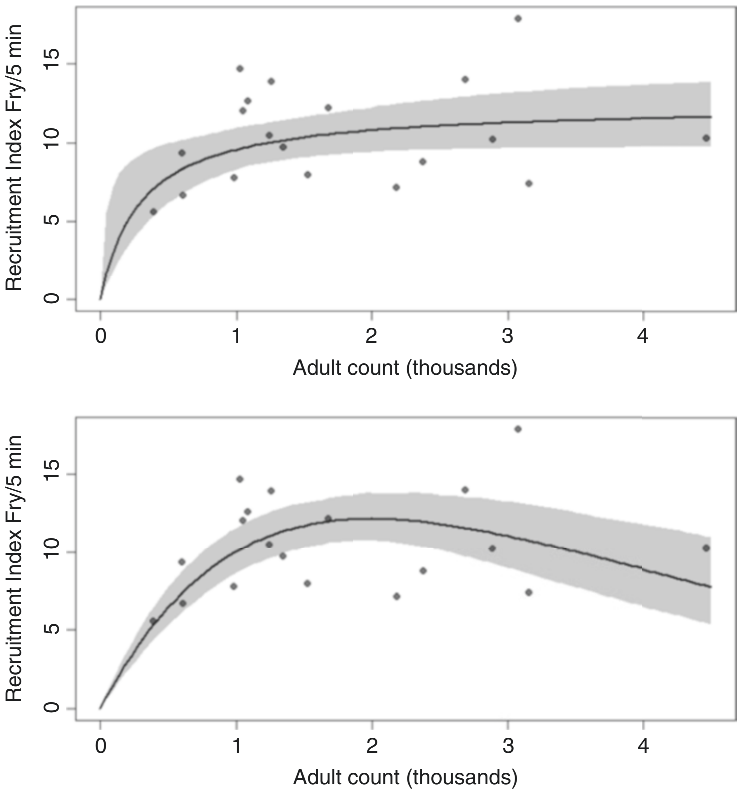

Fig. 7 Stock–recruitment curves fitted for River Maine brown trout, stock (adult count y^{-1}) and recruitment (semi-quantitative 0+ abundance index) datasets; grey shading indicates 95% confidence intervals; **a** (top) Beverton-Holt model; **b** (bottom) Ricker model

salmonid species and found that 71% showed density dependence in growth, whilst (Matte et al. 2020) indicated that density-dependent growth was stronger than survival in laboratory studies.

The River Maine data reflected a tentative stock–recruitment relationship. This was perhaps surprising since the recruitment measurement was based on a non-quantitative CPUE index of 0+ recruits instead of the more usual estimate of subsequent filial smolt or adult production. The S–R relationship on the River Maine was also surprising given that the stock estimate (adult count) was limited entirely to the migratory portion of the stock (e.g. the lake running dollaghan trout) and did not account for the potential contribution of sexually mature river resident trout. In anadromous trout populations, S–R relationships can often be confounded by the unknown effect of river resident brown trout spawners (Kennedy et al. 2017). Although resident brown trout may have contributed to fry recruitment across the River Maine monitoring network, the survey targeted areas accessible to, and dominated by, migratory dollaghan trout. In trout stocks with a migratory component, the migratory females are generally larger than con-specific residents and able to contribute more to overall ova production. Milner et al. (2006), for example suggested that migrant female sea trout were likely to be the dominant source of total egg production in most rivers with a migratory trout component.

Dome-shaped stock–recruitment curves have been described for some trout populations in Europe (Nicola et al. 2008; Elliott and Elliott 2006) whilst an asymptotic S-R model provided a better fit for a sea trout stock on the lacustrine Burrishoole catchment in Western Ireland (Poole et al. 2006). Many previous studies investigating the effects of density dependence on salmonid populations did so using stock–recruitment relationships of adult spawners against subsequent recruits (either smolts or adults) to infer density-dependent regulation on juvenile life stages (Marco-Rius et al. 2013). The monitoring of trout recruitment in the present study (0+ trout fry) occurred during the first summer and represented the earliest practical audit point in the life cycle to reflect recruitment, as soon as possible after the critical post-emergence regulatory density dependent period between 33 and 70 days (Elliott 1989). This early audit point may therefore better reflect the underlying S–R dynamic more closely than in later life stages after density-independent influences may have exerted further effects on the recruiting cohort (Kennedy et al. 2017).

A limitation with inferred studies can result from the sampling area being mismatched against the spatial range of the study species, such that the density estimate may not provide an adequate measure of competitive pressure, particularly if individuals can simply relocate from the limiting area to a new area (Berryman 2004). Previous work on the River Maine has shown that marked 0+ salmon were able to disperse extensively downstream by the following season (Kennedy et al. 2014) thus demonstrating the ability of young-of-year salmonids to relocate between habitats. Solomon (2006) postulated that dome-shaped S–R relationships were unlikely to be functional at a larger basin scale given the catchment-wide diversity of optimal and sub-optimal habitats available for dispersal and recruitment. Ray and Hastings (1996) furthermore suggested that the identification of functional density-dependent processes is more often hindered by inadequate spatial scaling than time series duration or test power. An advantage of the present study was that the extensive survey design exhaustively covered the total range available to migratory trout within the entire catchment and thus reflected recruitment status at the absolute maximum spatial scale. The fit of a dome-shaped model at the overall catchment scale was perhaps unexpected given the wide geographical range covered and the intrinsic ability of young trout to disperse within the river and therefore potentially ‘escape’ from density-dependent regulation. The survey design in the current study, although wide-ranging, located sampling sites sequentially on suitable shallow nursery habitats such that deeper adjacent sub-optimal habitats were not fully accessed. Ironically, despite the geographically exhaustive sampling regime, it may still be possible that the survey was not spatially exhaustive and that sub-optimal unsurveyed habitats could still have provided a refugia from density-dependent regulation. The (albeit inferred) existence of density-dependent-based regulation on the River Maine trout stock is still compelling, however, given the lack of alternative predictive relationships associated with the other available explanatory variables. A major anthropogenic pressure on the Maine stock is due to the commercial fishery which has harvested up to 30 tons of dollaghan from the lake each year. Although no significant relationship was evident between 0+ trout recruitment and commercial catch it is possible that the harvest may have decreased adult returns in some years, increasing the range and variability in spawner return rates and therefore stimulating the apparent S–R relationship observed in the stock.

Density-independent factors such as river discharge can also influence brown trout recruitment (Armstrong et al. 2003). Interestingly, a significant positive correlation was observed between 0+ trout and 0+ salmon recruitment on the River Maine, perhaps suggestive of common environmental conditions influencing the success of emergent salmonid cohorts? A distinct parabolic relationship has been documented elsewhere between the flows evident upon alevin emergence and subsequent trout recruitment, in which low and high flows corresponded with reduced recruitment whilst medium flows tended to associate with better recruitment. This phenomenon has been observed in brown trout populations across a number of other countries and throughout the natural range of the species (Cattanéo et al. 2002; Richard et al. 2015; Lobón-Cerviá et al. 2017). The ecological mechanisms underlying such a parabolic relationship between recruitment and spring flows may be linked to reduced habitat quantity for young-of-year juveniles in drought years and wash-out of emergent fry in high discharge years (Heggenes and Traaen 1988). Lobón-Cerviá et al. (2017) argued that the consistent identification of stream discharge as a predictor of annual recruitment, across many different stream types and life history strategies, provided compelling evidence for it to be considered as the main underlying 'modus operandi' for trout recruitment. The River Maine lacked any clear association between trout recruitment and river discharge, particularly for the flows experienced by emerging juveniles in April or May. The climate in Northern Ireland is mild and wet with high exposure to rain bearing winds off the Atlantic Ocean and average annual rainfall totals of between 800 and 2000 mm (UK Met Office). A consequence of these consistent rainfall patterns is that true drought periods, evident in other regions, are highly unusual in Northern Ireland. When dry spells do occur in Northern Ireland they are generally in summer, outside the key period between spawning and emergence of salmonids, and being on the northeast Atlantic seaboard of Europe, high summer river temperatures threatening to salmonid fish are as yet extremely rare. Recruitment limitation, consequential to low stream flow conditions post-alevin emergence, was not observed on the River Maine. In fact, the highest trout recruitment years recorded in the Maine catchment (2017, 2020) actually resulted from the driest springs, confounding a parabolic relationship between discharge and recruitment. It should be noted however, that the River Maine was subject to extensive anthropogenic pressures, including the commercial fishery, but also a major arterial drainage scheme in the 1970–1980s which modified the channel topography and hydrology (Essery and Wilcock 1990). It is entirely possible that the modified post-drainage channel morphology and discharge patterns may have altered, weakened or unnaturally influenced the relationship between trout recruitment and flow on the river.

5 Conclusions

The current study illustrates the benefit of long-term monitoring programmes which provide an important basis for describing and understanding short-term fluctuations and trends (Euzenat et al. 2006). The work also indicates the potential of resource-efficient semi-quantitative electric fishing methods to build long-term recruitment monitoring datasets. Traditional, quantitative, depletion electric fishing methods are resource heavy in comparison to the semi-quantitative method which is rapid, portable and can facilitate up to 15 sites per day using a two-person crew (Crozier and Kennedy 1994). A large river catchment like the River Maine can thus potentially be fully surveyed using SQ techniques in c. 2 weeks per year. The recruitment index of 0+ trout on the River Maine was linked to the previous adult spawning cohort through a S–R relationship rather than environmental parameters such as spring flows. The S–R relationship outlined in the River Maine case study may have been heavily influenced or even generated by local, anthropogenic factors and this will require further targeted investigation and assessment.

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