LONG TERM ABUNDANCE PATTERNS OF POTAMODROMOUS BROWN TROUT IN A LARGE LACUSTRINE CATCHMENT IN COUNTY FERMANAGH

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ABSTRACT

Long~~-~~-term survey data detailing brown trout abundance in the Lough Erne catchment in Co. Fermanagh were tabulated from 1968–2016. These data included redd counts and electric fishing surveys across three key spawning tributaries in addition to gill-net surveys of the lake. The abundance of spawning adults fluctuated widely across the time-series and were examined in relation to various pressures, including a major disease epidemic and the invasion of the catchment by zebra mussels. A functional stock-recruitment relationship between adult spawners and young-of-year juveniles in the spawning tributaries was identified and described. Redd counts were significantly lower for the post~~-~~-zebra mussel time-series (2000–~~20~~16) than the pre-zebra mussel time-series (1968–~~19~~99). The post~~-~~-zebra mussel invasion period was associated with increased water clarity, reduced plankton productivity and changes to the balance of coarse fish species in the lake. The significance of these changes ~~are~~ is discussed in relation to the trout stock.

INTRODUCTION

Potamodromous (lake running) brown trout (*Salmo trutta* L.) populations represent a significant ecological, economic and recreational resource in Ireland. Lake trout angling contributes significantly to the Irish economy (TDI~~,~~ 2013; O'Reilly~~,~~ 2015) and in Northern Ireland potamodromous trout are commercially fished in Lough Neagh. Lake running trout stocks encounter a diverse range of pressures including predation, anthropogenic exploitation, habitat perturbation, compromised water quality and climate change (George *et al*.~~,~~ 2010). Recent invasive aquatic species may also pose risks for Irish lake trout with exotics such as curly pondweed (*Lagarosiphon major* Ridley) and zebra mussels (*Dreissena polymorpha* Pallas) influencing the ecology of some modern Irish waterbodies (MacNeil *et al*~~,~~. 1999; Maguire *et al*. 2003; Millane *et al*. 2012).

Constraints on historical and contemporary survey and assessment infrastructure~~,~~ mean that many fish stocks are described as 'data-limited' (Shephard *et al*. 2019). Irish lake running trout stocks are often data-limited, with potential stock assessment information such as angling returns or commercial harvest data, either short term, patchy or absent. Catch data can be further limited by a paucity of effort and catchability statistics to complement catch returns. In addition to data limitation, potamodromous trout are challenging to assess because they may inhabit multiple spawning tributaries within a lake catchment and may exhibit highly variable life history dynamics within and between tributaries (Ferguson and Taggart~~,~~ 1991; Massa-Gallucci *et al*. 2010). Consistent, ~~long term~~long-term data, describing the abundance of Irish lake trout at a catchment scale are highly valuable but unfortunately relatively rare and often unpublished.

Lower Lough Erne in ~~County~~ Co. Fermanagh has a significant stock of lake running trout and is currently managed by the Department of Agriculture, Environment and Rural Affairs (DAERA) for Northern Ireland as a wild game fishery. The Erne trout stock has been supplemented with periodic enhancement stocking mostly using young-of-year (0+ age class) trout stocked into the influent tributaries (Ferguson and Taggart~~,~~ 1991); this work was discontinued ~~post~~ in 2015 with the closure of the local hatchery facility. Lower Lough Erne suffered a severe ecological perturbation in the late 1990~~'~~s following the introduction, colonisation and establishment of invasive zebra mussels (Rosell *et al*. 1999). Maguire *et al*. (2003) recorded a significant reduction in the mean total phosphorus concentrations in Lower Lough Erne between 1998 and 2000 following the zebra mussel invasion.

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Historic time-series data detailing trout redd counts~~,~~ dating back to 1968~~,~~ were compiled for three major influent tributaries of Lower Lough Erne (Garvary, Ballinamallard and Kesh rivers). In addition, a range of complementary biological and environmental data from Lower Lough Erne were compiled across their respective available time-series (Vickers~~,~~ 1969; Cragg-Hine~~,~~ 1972; Kennedy and Strange~~,~~ 1978; Rosell *et al*. 1994; Crowley *et al*. 2001; Fisheries Conservancy Board for Northern Ireland Annual Reports; 1969–2007).

The main objectives of the current work were: 1) to describe the long~~-~~term status of brown trout in the Lower Lough Erne catchment; 2) to test the hypothesis that trout abundance has remained unchanged before and after the invasion of zebra mussels in Lower Lough Erne assuming the year 2000 as a ~~break-point~~breakpoint; 3) to identify any correlations between the trout abundance time-series and available environmental time-series.

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MATERIALS AND METHODS

STUDY AREA

The Lower Lough Erne is located in ~~North West~~north-west Ireland, has a wetted area of 109.5~~-~~km^2 and maximum depth of 65m (Table I). The catchment rises on Slieve Glah mountain in ~~County~~ Co. Cavan and discharges into the Atlantic Ocean at Ballyshannon, Co. Donegal. The underlying geology is dominated by carboniferous limestones. Upper and Lower Lough Erne form major lakes on the system which host over 150 islands. The lakes have several feeder tributaries including the Garvary, Kesh, Ballinamallard and Colebrooke rivers, all of which support populations of brown trout (Fig. 1). The outflow from the lake has an average daily discharge of *c*. 100 m^{3}s^{-1} and supports two run of river hydro-electric stations at Cliff and Ballyshannon. Lower Lough Erne is an important recreational fishery ~~which~~ that attracts many brown trout anglers, particularly in the late spring during the mayfly hatch.

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Redd ~~Counts~~counts

Historical trout redd count information was collated for the main spawning tributaries of Lower Lough Erne, including the Garvary, Kesh and Ballinamallard rivers. These data were obtained from archived annual reports of the Fisheries Conservancy Board (FCB) for Northern Ireland and included the period from 1968 until 2007, when the organisation was abolished. After 2007 DAERA inland fisheries enforcement staff continued to conduct a redd count, but only on the Garvary river. The quality of the historical redd count data was investigated by interviewing former FCB employees to determine details of the survey design, surveyors, areas covered and time-series consistency. The trout redd surveys were conducted annually across standard locations and included catchment areas accessible to migratory salmonids (i.e. excluded areas above impassable barriers). The redd count coverage included the perceived entirety of spawning habitats on the Garvary river and a consistent sample of the main known spawning grounds on the Kesh and Ballinamallard rivers. The survey design on each river was classified as a single pass peak count (Gallagher *et al*. 2007) as trout redds were counted once during November before the salmon (*Salmo salar* L.) spawning period which, in the Erne system, generally extends from mid-December to early January. The trout redd counts were treated as minimum estimates because observer error could not be ascertained, particularly for the historical data. In some years data were not collected if protracted elevated discharge conditions prevented identification of redds. The survey on each river was undertaken by 1–2 fisheries staff each year. The Garvary count was undertaken by the same individual from 1968 to the early 1990s when a new officer shadowed the original surveyor for *c*. ~~4~~ four years before collating the time-series until present. Two staff were involved in the Kesh work and the Ballinamallard redd count was conducted by the same person across the entire time-series.

The redd count data were tabulated and collated into time series to provide an index of spawning trout abundance for each river. The trend over time for each river was examined using Mann-Kendall time-series analysis to detect any upward or downward monotonic trend, with a null hypothesis that there was no trend (Hirsch *et al*~~,~~. 1982). The analysis was undertaken for two discrete time periods~~.~~: ~~Initially~~ first, the full series from 1968-present was examined and ~~secondly~~ second, the series ~~post-~~after 1974 was analysed to exclude the effect of the historical Ulcerative Dermal Necrosis (UDN) outbreak. The significance level of the Mann-Kendall test was altered using the Bonferroni correction factor (*alpha altered* = 0.05/3 = 0.0167) to take account of the multiple tests and protect against Type I error. The mean redd count for 1968–~~19~~99 for each river was also compared against the ~~post~~ period after 1999 ~~period~~ using a non-parametric Mann-Whitney U test.

Survey ~~Netting~~ netting ~~Data~~data

The fish stocks of Lower Lough Erne have been monitored on a regular (2–~~4 year~~4-year intervals) basis since 1991, using multi-mesh survey gill nets to capture a sample of all species and sizes of fish, with fixed survey sites located at locations in water depths down to 10m (Rosell~~,~~ 1994). Rosell (1994; 2000) outlined the location of the standard survey sites, calculation of catch per unit (CPUE) metrics and sampling methodology. The dataset covered the period 1991–2016 and includes counts of brown trout in addition to several other commonly encountered species/hybrids including; pike *Esox Lucius* L., perch *Perca fluviatilis* L., Roach *Rutilus rutilus* L., Bream *Abramis brama* L., and roach x bream hybrids. Brown trout abundance data from the gill net surveys were available for the period 1992–

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2016 and provided a relative abundance (CPUE) metric, standardised between years as the number of trout/ meter survey net.

Electrofishing data

A range of historical fully quantitative (FQ) electrofishing data were obtained from published studies describing the mean annual density of young-of-year (0+ age class) trout parr in tributaries of Lower Lough Erne during summer. These data were derived from standard long-term monitoring sites on the Garvary (2 sites), Kesh (3 sites) and Ballinamallard (3 sites) rivers (Table II). Data from 1968–9 were collected with the Petersen mark-recapture technique (Vickers, 1969) employed to determine the efficiency of fishing and estimate of the most probable number of fish per 100m^2 (Cuinat, 1967). Data from 1976 onwards were collected by multiple pass, depletion electric fishing (Kennedy and Strange, 1978) to determine the density of juvenile trout present at each survey site. The depletion electric fishing surveys used a minimum of 3 fishing passes with the survey area enclosed by fine mesh stop nets and employing one electric fishing backpack for each 4m of channel width surveyed. All fish collected during the surveys were identified to species, measured for fork length (mm) and a scale sample taken from some individuals to determine annual length thresholds between 0+ and >0+ trout. Fish density by age class (0+, >0+) was determined from depletion data (Zippin, 1958) and expressed as number fish per 100 m^2 of surveyed habitat. The quantitative electric fishing data, although temporally sporadic, and spanning a range of surveyors and 2 techniques provided standardised information on juvenile population densities dating back to 1968. The annual density of 0+ trout for each tributary over time was plotted. Electric fishing data were analysed using the non-parametric Mann-Kendall test (Mann, 1945) applied to the seven temporal observations recorded from 1968 to 2014 to detect monotonic trend at individual sites. The R package Kendall (McLeod, 2011) was used to conduct the analysis. In order to protect against Type 1 error when assessing trend a Bonferroni correction factor was applied to the level of significance. The focus on 0+ trout was a consequence of the potamodromous habit of Erne trout stocks since densities of 1+ and older fish are often depleted due to outward lake emigration (Vickers, 1969).

A second electric fishing data series was compiled for the Garvary river. These data were derived from 5-minute timed semi-quantitative (SQ) electric fishing (Crozier and Kennedy, 2004) surveys undertaken on the Garvary river from 2005–2016. This survey was conducted across 10 fixed sites each August/September and provided a relative index of 0+ trout abundance on the river, defined as the annual number of 0+ trout fry 5 mins^{-1} site^{-1}. SQ sites were distributed through-out the river channel at a density of *c.* 1 site/800m channel length and surveyed shallow nursery/riffle habitats <40cm depth. The available 12 year12-year SQ time- series was supplemented by older quantitative survey results which that were back-transformed into SQ estimates using a linear regression model relating SQ values (no. / 5 mins) to fish density (no. per m^2) and derived from lake and sea running trout stocks across Northern. Ireland (Kennedy *et al.* 2017). The Garvary electric fishing dataset thus provided a longer term, more complete index of trout recruitment on a primary Lough Erne spawning tributary. The Garvary recruitment dataset was investigated for possible explanatory relationships against an index of adult spawner abundance (redd count) from the previous year. The Ricker curve (Ricker, 1954) has been frequently shown to provide the best model for *Salmo trutta* stock recruitment relationships (Elliott, 1985; 1987; Elliott and Elliott, 2006; Nicola *et al*. 2008) and was applied to explore any possible relationship between the Garvary redd count and subsequent recruitment;:

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

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

Supplementary ~~Data~~ data and ~~Cross~~ cross ~~Correlation~~ correlation ~~Analysis~~analysis

Stocking data was compiled from DAERA for the period 1968–2015. The total number of brown trout stocked into the Erne catchment was collated by year and life stage, tabulated and converted into a historical time-series.

A range of environmental data were also collated into time-series. Water samples have been taken from Lower Lough Erne fortnightly at five sites since 1990. Samples were routinely analysed for various environmental parameters including suspended solids (mg/l), chlorophyll *a* (mg/l) conductivity (µS), dissolved oxygen saturation (%) and temperature (ºC). Mean annual surface values for each environmental variable were used in the current study whilst oxygen and temperature datasets included measurements from two different depths (surface and 5m). Further details on the Lower Lough Erne water chemistry sampling programme are available through the Environmental Change Network (Rennie *et al*. 2006) and the analytical methods employed for the long-term Lough Erne sampling are described by Foy *et al*. (1993) and Qixing *et al.* (2000).

Redd counts were assumed to reflect the relative abundance of spawning trout ~~which~~ that had completed a period of residence in Lough Erne. The trout redd count time-series from each river were tested for correlation with other potential explanatory variables including~~;~~: stocking numbers, suspended solids, chlorophyll *a*, conductivity, dissolved oxygen (surface and 5m) and temperature (surface and 5 m). Some potential time-series data such as species specific gill-netting CPUE results were too ~~patchy~~sparse with insufficient data to undertake robust analysis and therefore were excluded. Cross-correlation analysis was undertaken at various time lags including lag 0 (synchronous time-series) and at increasing time lags 1–4 (explanatory variables offset by 1 to 4 years). Prior to correlation analysis the time-series data were assessed for stationarity. Autocorrelation was noted for several of the time series including Ballinamallard Redd Count, Garvary Redd Count and Chorophyll *a*. These time series were treated (pre-whitened) using an autoregressive integrated moving average (ARIMA) model to eliminate any non-stationarity. The autoregressive model pre-whitened the time-series with a first order correction, i.e. accounting for a correlation between the current time point and the previous time point. After the time-series were pre-whitened, stationarity was achieved. Cross-correlation analysis was undertaken in Genstat version 10 and any significant correlations were identified and extracted.

RESULTS

Redd ~~Counts~~counts

The surveyed spawning areas on the Garvary river were assumed to cover all the available reproductive habitats on the river. When mapped onto a Geographical Information System (Arcview 3.2) around 2 km of channel ~~were~~ was surveyed each year, representing *c*. 23% of the total accessible channel length. The Garvary river is an important spawning tributary for potamodromous trout in Lower Lough Erne and exhibited a mean redd count of 276 redds yr^{-1} and ranged from 50 redds (1972) to 510 redds (1985) across the 48-year time period (Fig. 2a). The redd density in the river was *c*. 0.14 redd/m spawning habitat or *c*. 0.03 redd/m total

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river length. The Garvary redd count between 1970 and 1974 reflected a much lower abundance of spawning trout with a mean value of only 86 redds yr^{-1} (+/- 29, 95% Confidence ~~Interval~~interval (C.I.)), due to a major outbreak of ~~Ulcerative Dermal Necrosis (~~UDN~~)~~ disease at that time. The ~~23 year~~23-year period from 1975–~~19~~97 represented a relatively high and stable period of spawner abundance with a mean count of 375 redds yr^{-1} (+/- 53, 95% C.I.). A decline in redd numbers was then evident in the period from 2000–~~20~~15 during which the mean count dropped to 189 redds yr^{-1} (+/- 23, 95% C.I.). There was no significant monotonic trend detected when the full Garvary time-series (1968–2015) was examined but a significant decreasing monotonic trend was observed on the river ~~post-~~after 1974 (Z=-3.358, P=0.001). The Kesh and Ballinamallard rivers exhibited mean annual redd counts of 174 and 166 redds yr^{-1} respectively (Fig. 2-b,c). Analysis of the time-series ~~post-~~after 1974 indicated a significant decreasing monotonic trend in redd abundance on the Kesh river (Z=-2.421, P=0.015). Although the redd count declined, the monotonic trend was not significant on the Ballinamallard river (Z=-2.007, P=0.045). Comparison of the redd count data for each river, inclusive of all years in each time-series, indicated a significantly lower redd count post 1999 (Table III) across all three study catchments (U-Test; all $P < 0.05$).

Survey ~~Netting~~ netting ~~Data~~data

The CPUE (number/m survey net) of brown trout captured in the marginal survey netting programme declined during the available time-series from 1992–2016 (Fig. 3). Linear regression analysis of brown trout CPUE against time indicated a significant decline across the available time series (Least Squares Regression, $R^2 = 0.68$, $P < 0.05$). Although the mean CPUE pre-2000 (0.014 trout/m) was 40% higher than post 1999 levels (0.010 trout/m) too few data points were available pre-2000 (1992 and 1996) to facilitate a robust statistical comparison of trout CPUE before and after zebra mussel colonisation.

Electric ~~Fishing~~ fishing ~~Surveys~~surveys

Quantitative electric fishing data showed that the mean annual 0+ trout density at sites across the Lower Lough Erne catchment varied markedly across all the monitored tributaries (Fig. 4a-c). A significant monotonic increasing trend was detected at the Kesh river site 3 (S=19~~;~~, P = 0.007). No significant trend was detected at any of the other ~~7~~ seven sites although it should be noted these results were based on relatively sparse time-series.

The more detailed SQ electric fishing abundance index for the Garvary river also demonstrated high year-on-year variability ranging from < 6 0+ trout 5 min^{-1} in 1988 to > 25 0+ trout 5 min^{-1} in 1969 and 2014 (Fig. 5). Relatively high inter-annual variability was apparent across the SQ time-series but no significant difference was detected in fry numbers between the periods 1968–~~19~~99 and 2000–~~20~~16. Modelling of the Garvary redd counts against the SQ electric fishing index in the following year revealed that a Ricker type curvilinear stock-recruitment (SR) relationship was evident and successfully explained 45% of the variance in the relationship between stock and recruitment (Fig. 6). The good fit of the Ricker model was indicative of a functional stock-recruitment relationship influencing the Garvary trout population. The asymptotic level of fry recruitment, as determined from the Ricker model, was attained around a spawning stock abundance level of *c*. 162 redds.

Supplementary ~~Data~~ data and ~~Cross~~ cross ~~Correlation~~ correlation ~~Analysis~~analysis

Stocking was undertaken intermittently between 1968 and 2015 using various life stages of trout (ova, fry, fingerlings and yearlings). The heaviest stocking year was 2006 when 1.25

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million fry and summerlings were stocked into the catchment (Fig. 7) and across the time-series in excess of 19.8 million individuals were stocked.

The concentration of total suspended solids (inclusive of both organic and inorganic fractions) and chlorophyll *a* exhibited high variability and both declined significantly across their respective time-series (Fig. 8) with significantly lower concentrations post 1999 in comparison to earlier years (Table II). Suspended solids and chlorophyll *a* are useful indicators of water clarity with reduced levels indicative of increased water clarity. Although surface water temperature was slightly higher across more recent years (Table II) the relative infrequency of long-term temperature measurements prevented more detailed analysis of thermal habitat suitability for trout.

Cross correlation analysis showed several significant relationships between trout abundance and potential explanatory variables. A significant positive correlation was found between Chlorophyll *a* concentration and the trout redd count on the Kesh river at a lag time of 0 (r=0.405, n=47, P=0.003). A significant negative relationship was identified between surface water temperature and both the Garvary (r= - 0.299, n=47, P=0.021) and Kesh (r= - 0.333, n=48, P=0.011) redd counts in the following year.

DISCUSSION

The stock of lake running brown trout in Lower Lough Erne has fluctuated widely between 1968–2016 and has been negatively impacted by two major disturbance events during that period. The initial disturbance was due to a widespread disease epidemic (UDN), which seriously reduced adult salmonid populations in Lower Lough Erne in the early 1970~~'~~s (Kennedy and Strange~~,~~ 1978) but from which stocks fully recovered after several years.

The second and perhaps more pernicious perturbation occurred ~~post~~ after 1999 and co~~-~~incided with a turbulent period in the ecology of the lake after the establishment of invasive zebra mussels. The trout redd count and survey netting data suggest that adult trout abundance declined following the zebra mussel invasion with spawning trout effectively experiencing a phase shift to a lower baseline of abundance ~~post~~ after 1999.

Much of the Erne data is based on redd counting and an important assumption with these data are that they adequately reflect the background level of spawning adults in the population. Redd count data can however be subject to sampling error due to surveyor inexperience, incorrect redd identification, poor water visibility or inadequate survey coverage (Rieman and McIntyre 1996; Rieman and Myers~~,~~ 1997). Maxwell (1999) suggested that the potential sampling errors associated with redd counting made the technique less suitable for fine scale annual stock assessment and more suitable for detecting larger scale changes in trout abundance. Dunham *et al*. (2001) also indicated that redd counts were useful for reflecting substantial changes in population sizes when long-term trends outweigh potential ~~short term~~short-term errors. The Erne redd count time-series had several advantages in that a relatively small, consistent and inter-calibrated pool of experienced staff conducted the work, a significant proportion of spawning habitat was consistently sampled each year and that counts were not attempted in high discharge years. In addition, the substantial 'phase-shift' change in redd abundance on the Erne was recorded independently on all the tributaries and over the same time~~-~~period.

Long term studies of brown trout population dynamics conducted on other lakes have shown that stocks can be influenced by a range of factors and pressures. In Lake Songsjoen, Norway, a ~~27 year~~27-year study indicated that the spawning stock was controlled largely by density dependant mortality and fishing pressure (Langeland and Pedersen~~,~~ 2000). A longer term ~~50 year~~50-year study in lake Ovre, Norway, showed that a major reduction in the lake trout stock and lower recruitment into the lake, was related to the introduction of another invasive species, the European minnow, *Phoxinus phoxinus*, L., (Borgstrøm *et al*. 2010). Decreased redd counts in Lower Lough Erne tributaries occurred after the establishment of an invasive species. Zebra mussels were initially observed in Lower Lough Erne around 1996 and within 2–3 years had spread rapidly throughout the system, extensively colonising all available hard substratum (Rosell *et al.* 1999). The mussels exerted considerable influence on the ecology of the lake, extensively filter feeding local phytoplankton communities, reducing total phosphorus levels and clearing the water column (Maguire *et al*. 2003). Zebra mussel establishment in the late 1990s also caused water clarification through reduced algal crops and major reductions in zooplankton biomass (Maguire *et al.* 2003).

The removal of large quantities of suspended material from the water column by zebra mussels can radically lower plankton abundance and increase water transparency (Holland~~,~~ 1993). The positive correlation of redd counts with chlorophyll *a* is indicative of a potential linkage between lake trout abundance and the ecological consequences of zebra mussels. Decreased phytoplankton (chlorophyll *a*) and suspended solid levels are intrinsically linked with increased water clarity and subsequent knock on effects for lake ecology. Zebra mussels have significantly reduced zooplankton in lakes where they have become established (Higgins and Vander Zanden~~,~~ 2010), which can reduce the feeding opportunities, growth and condition particularly for young 0+ lacustrine fish (Nienhuis *et al*. 2014). Guiliano (2011) for example, showed that the growth and condition of 0+ rainbow trout (*Oncorhynchus mykiss*, Walbaum, 1792) decreased due to diet changes after zebra mussel invasion of a Michigan catchment. Nienhuis *et al*. (2014) further showed that there was significantly better growth of North American lake trout (*Salvelinus namaycush*, Walbaum, 1792) in lakes without zebra mussels in comparison to those ~~which~~ that had been invaded. Insufficient data are currently available to examine the details of Erne trout diet but a ~~food based~~food-based impact on 0+ brown trout in the lake seems unlikely as the juvenile fish are produced in the influent rivers and only enter the lake after 2–4 years.

The zebra mussel invasion of Lough Erne also co~~-~~incided with the start of a long-term increase in the perch stock, which by 2016 had replaced roach as the dominant fish species by number and had almost reached parity with roach in terms of biomass (DAERA~~,~~ 2019). It is worth noting that at the start of the available data series for on trout, roach were recently established in Upper and Lower Lough Erne (Cragg-Hine~~,~~ 1973~~,~~; Fitzmaurice 1981), and rapidly became the most abundant fish species the lake in terms of both biomass and numbers (Rosell~~,~~ 1994).

Increased water clarity in lakes can also increase the predation risk of prey fish to larger piscivorous predators (Snickars *et al*. 2004; Skov *et al.* 2007). Improved water clarity in Lower Lough Erne and increased susceptibility of trout to local visual predators such as cormorants (*Phalacrocorax carbo* L.) or northern pike (*Esox lucius* L.) could represent a contributory mechanism behind the phase-shift in lake trout abundance.

Pike have been present in Lough Erne since at least the 1800s (Newland~~,~~ 1851;~~,~~ Grimble~~,~~1913). They have traditionally been controlled by removal in several Irish trout lake fisheries including Lough Erne, although with reduced levels of harvest over the past 30 years from over 20 tonnes per year in the 1960s to ~~circa~~ *c.* 5 tonnes annually at present. (Rosell and MacOscar~~,~~ 2002~~,~~; DAERA Inland Fisheries, ~~Pers~~pers.~~,~~ c~~C~~omm.). Pike have been shown to shift diets to include roach since the introduction of the latter to Irish lakes (McLoone *et al.* 2018), complicating the understanding of their impact on trout (Fitzgerald *et al.* 2019). Given probable changes in predator-prey relationships between pike, trout, perch and roach, particularly since the arrival of zebra mussel, ascertaining current predation rates on trout in Lower Lough Erne may require updated and careful investigation, possibly through the application modern fish telemetry methods.

The mean annual surface water temperature in Lower Lough Erne had a negative correlation with some trout redd abundance metrics. Ambient temperature modulates the physiology, energy balance and behaviour of poikilothermic fish like brown trout (Elliott and Hurley~~,~~ 2000; Elliott and Elliott~~,~~ 2010). The impacts of increasing water temperatures on lake fish are diverse and could include changes to growth, behaviour, availability of suitable habitat or altered susceptibility to competition (Murdock and Power~~,~~ 2013; Connor *et al*. 2019). The potential interplay between climate change and increased water clarity is also important and may increase temperature impacts on lacustrine communities. ~~(~~Rose *et al*. (2016) for example, showed that climate change driven increases in lake water temperature could be further exacerbated by improved water clarity. Brown trout are a highly adaptable species (Ferguson *et al.* 2019), tolerant of a wider thermal niche than some other sub~~-~~arctic fish species and have been shown to replace sympatric stenothermic species as climate warms in northern hemisphere freshwaters (Al-Chokhachy *et al*. 2015; Morrissey-McCaffrey *et al*. 2019). It was beyond the scope of the present study to differentiate the physiological, ecological and behavioural consequences of increasing temperature on brown trout in Lower Lough Erne. The resilience of Irish lake dwelling brown trout to climate change however requires further investigation to model impacts, predict potential consequences and elicit suitable management behaviours.

Enhancement stocking with hatchery reared brown trout has been shown to be largely ineffective across a wide range of case studies (Caudron *et al*. 2004; Ruzzante *et al.* 2004; Linløkken *et al*. 2019). The historical stocking programme on the Erne used hatchery origin trout and was found to be particularly unsuccessful. Kennedy and Strange (1978) for example, showed that 5 separate stockings of Lower Lough Erne with 7,463 tagged hatchery trout (conducted between 1969—~~19~~76), resulted in only 8 fish (0.11%) being recaptured by anglers. Taggart and Ferguson (1986) undertook an electrophoretic genetic evaluation of the Lower Lough Erne stocking programme from 1969–~~19~~83 and showed that by the early 1980~~'~~s the Lower Lough Erne trout stock exhibited a substantial hatchery component with 21.5% of lake captured fish found to be of hatchery origin. Stocking with hatchery fish can pose risks to the supplemented wild stock through gene introgression, dilution of the native gene pool and potential loss of fitness (Satake *et al.* 2012). The introgression of non-native genetic material into the wild population was identified as a major threat to the Erne stock (Taggart and Ferguson~~,~~ 1986) and the introduction of hatchery brown trout was discontinued after the early 1980~~'~~s. The stocking programme was revived between 1998—2015 and used indigenous native Erne broodstock with the resultant progeny stocked into the lake tributaries. Recent unpublished work has indicated that the genetic signature of hatchery

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brown trout, amongst Erne trout samples, decreased notably between 2000–2011 (P. Prodohl, pers. comm.), which augers well for the future genetic integrity of the stock.

The Garvary river was maintained as a control catchment with stocking activities prohibited and thus reflective of wild trout recruitment. The similarity in the redd count trend between the unstocked Garvary and the other stocked tributaries (Fig. 2) indicated that the enhancement programme did not appear to differentially alter adult returns amongst the tributaries and that widespread natural factors were probably more significant drivers of trout population dynamics across the Erne catchment.

The current study appears to suffer a major contradiction between the decline in adult Erne lake trout (spawners) in the Erne post- after 1999 and the production of juvenile trout (recruits) in the feeder streams which that remained paradoxically stable. The explanation for this apparent contradiction is due to the functional association between the two life stages, which occupy different habitats but are intrinsically linked through a stock-recruitment relationship. Salmonid populations naturally overproduce and since the young fish are highly territorial within their riverine nursery habitats (Elliott, 1989) each recruiting cohort is limited to a specific carrying capacity by the availability of individual territories (i.e. stream habitat abundance/quality) (Kelly-Quinn and Bracken, 1988; Armstrong *et al.* 2003). The deposition of more eggs than the carrying capacity of a stream can support therefore provides no additional benefit to recruitment and may actually depress subsequent production through increased competition for limited resources. A range of trout stocks have been shown to exhibit such dome shaped, asymptotic, stock-recruitment relationships across various river and lake catchments (Elliott and Elliott, 2006; Euzenat *et al*. 2006; Poole *et al.* 2006; Kennedy *et. al.* 2017). The Garvary river also exhibited a dome shaped stock-recruitment relationship between the spawning stock and subsequent young-of-year recruitment, with the maximum recruitment evident at medium stock levels (162 redds yr^{-1}). At higher, historic levels of spawning stock abundance (> 350 redds yr^{-1}) the young-of-year recruitment was limited by the spatially finite habitat resources and intense competition between emergent 0+ age class fry. In more recent times (postafter- 1999) young-of-year recruitment has been maintained by lower numbers of spawners (> 180 redds yr^{-1}). The reduced stock of Lough lake trout, after the downward phase shift post after 1999, may still be capable of maintaining an asymptotic level of recruitment in the spawning tributaries. This relationship also suggests that decreased abundance of adult lake running trout is less due to issues with riverine production than to issues in the lake going phase of the life-cyclelife cycle.

Long term data from Lower Lough Erne has indicated that lake running trout stocks have declined towards a lower abundance level post after 1999. Despite significant anthropogenic manipulation of trout stocks via stocking no improvement in abundance was realised. The main perturbations on the Erne stock have been associated with widescale biological phenomena including disease epidemics and the establishment of an invasive species. The interaction between trout stocks, zebra mussel invasion, water clarification, reduced plankton productivity, changes in balance between other fish species including competitors and predators is likely to be complex and there is no single obvious driving mechanism of the reduced trout stock, other than that by elimination the impact causing recent decline appears to be on trout in the lake phase. Climate change may be influencing environmental parameters in Lower Lough Erne and may interact with other factors to further

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pressure the native fish community. The maintenance of healthy, productive brown trout stocks is an important objective for Irish fishery managers. Future management activities should be focused on the conservation of adult trout, enhancement and protection of habitats, water quality and biosecurity instead of the historical reliance on extensive restocking programmes. Future research is also required to quantify the ecological consequences of increased lacustrine water clarity on trout stocks and to investigate the interactions between climate change and other potential stressors.

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