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The changing times of Europe's largest remaining commercially harvested population of eel *Anguilla anguilla* L.

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Abstract

This study quantifies the processes involved in regulating the European eel population of Lough Neagh, a lake in Northern Ireland. The relationship between glass eel input and silver eel output for the 1923–1997 cohorts was best described by a Beverton–Holt stock recruitment model. Glass eel input time series was not complete and was thus derived from the relationship between catches elsewhere in Europe and Lough Neagh, together with the addition of stocked glass eel. Silver eel output was the sum of silver eel escapement, catch and yellow eel catch converted to silver eel equivalents. Natural mortality increased with glass eel density, ranging from 0.017 to 0.142 year^{-1}. The mean carrying capacity increased from ≈3.25 M silver eels (≈26 kg ha^{-1}) for the 1923–1943 cohorts to ≈5.0 M (≈40 kg ha^{-1}) for the 1948–1971 cohorts before regressing back to ≈3.25 M. The total silver eel output was highest during the late 1970s/early 1980s at 35–45 kg ha^{-1} year^{-1} and lowest during the early years of the 20th century and is currently at 10–15 kg ha^{-1} year^{-1}. The findings are discussed in relation to (a) the ecological changes that have occurred within the lough, associated with eutrophication and the introduction of roach (*Rutilus rutilus* L.), and (b) the decline of the wider European eel stock across its distribution range. The findings from this study have relevance for the wider management of the European eel stock.

KEYWORDS
European eel, exploitation, natural mortality, population dynamics, regime shift, stock recruitment

1 | INTRODUCTION

The European eel (*Anguilla anguilla*) stock is panmictic and can be regarded as a single stock throughout its entire range (Enbody *et al.*, 2021; Palm *et al.*, 2009). The status of the species is described by the International Council for the Exploration of the Seas (ICES) as remaining critical and is considered to be outside safe biological limits (ICES, 2018, 2019). The species has been listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) in 2007 and has been registered as critically endangered by the International Union for the Conservation of Nature and Natural Resources (IUCN) (Pike *et al.*, 2020). The decline in glass eel abundance

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commenced in the mid-1980s (Moriarty, 1986) approximately two decades after the decline in the spawning stock (Dekker, 2003) and is likely to have been caused by multiple factors (Dekker, 2004a). In 2007, the European Council issued Regulation (EC 1100/2007) which required Member States to (a) develop eel management plans (EMPs) for the recovery of the eel stock and bring in management measures with the aim of reducing anthropogenic sources of mortality and increasing the abundance of spawners, and (b) set the specific target whereby 'at least 40% of the silver eel biomass relative to the best estimate of escapement that would exist if no anthropogenic influences had impacted on the stock'. The targeting and effectiveness of such measures can be improved through knowledge of the ecological processes underlying the dynamics of the population and the abiotic and biotic factors influencing them. The individual processes involved have been the subject of numerous reviews and include growth (Boulenger *et al*., 2016; Daverat *et al*., 2012; Tesch, 2003), age at maturity (Bevacqua *et al*., 2006; Svedäng *et al*., 1996; Vøllestad, 1992), gender differentiation (Davey & Jellyman, 2005; Geffroy & Bardonnet, 2016), upstream dispersal (Feunteun *et al*., 2003; Ibbotson *et al*., 2002) and mortality (Bevacqua *et al*., 2011). Bevacqua *et al*. (2019) has shown how such data can be brought together to provide a better understanding of the processes affecting a population and then used to help guide management measures.

European eels are believed to spawn in the Sargasso Sea (McCleave *et al*., 1987; Tesch & Wegner, 1990). The eggs hatch as leptocephalus larvae and drift across the Atlantic Ocean to the continental shelf of Europe, where they metamorphose into post-larval, transparent glass eels and migrate towards and into estuaries (Cresci, 2020; Tesch, 2003). Glass eels migrate upstream in shoals, their shoaling behaviour changing from passive migration to active migration during the migration season (Harrison *et al*., 2014). This immigration phase is generally followed by a settlement period and metamorphosis into the pigmented elver stage and the start of feeding (Tesch, 2003), after which they embark on a secondary active migration in early summer, which is strongly influenced by temperature (White & Knights, 1997a, 1997b), and commence the juvenile yellow eel phase. After a period of time the yellow eels mature into the silver eel stage and migrate downstream for spawning (Tesch, 2003).

Two key elements of population dynamics, where information is scarce, are: the influence of glass eel abundance on actual or potential silver eel output and the temporal stability of the regulatory processes (natural mortality and growth) affecting the production process. The impact of variability on abundance of subsequent life stages has been difficult to study as there are few locations where glass eel input and yellow eel production and/or silver eel output have been quantified over sufficiently long periods to account for the eel's longevity, which in some populations may be 30 years (Durif *et al*., 2009). Where this has been studied on the River Imsa (Norway) (Vøllestad & Jonsson, 1988) and Rio Esva (Spain) (Lobón-Cerviá & Iglesias, 2008) output has been found to be regulated by density-dependent processes.

Similarly, there have been few datasets suitable for the investigation of temporal stability in the regulatory processes (Dekker, 2004b; Poole *et al*., 1990, 2018). This is mainly due to the paucity of long-term data sets (Moriarty & Dekker, 1997). Dekker (2004b) modelled decadal changes in the yellow eel population in the Ijsselmeer (Netherlands). Whilst this was a comprehensive analysis, it did not identify the cause(s) of the additional mortality affecting the population, either from fishing or other sources of anthropogenic mortality or natural mortality. In terms of biological characteristics, Poole *et al*. (1990, 2018) in the Burrishoole system (Ireland) found an increase in the mean size of silver eels and a change in the sex ratio over a period of 30 years. This was possibly associated with a reduction in glass eel abundance and an increase in the productivity of the system.

An understanding of the dynamics of the population is needed to satisfy the central requirement of EC 1100/2007 of the 40% escapement target. One of the challenges set out in EC 1100/2007 is the baseline reference period. There is an underlying assumption in the Regulation that the baseline reference period is stable and in Article 5(a) it is defined as 'prior to 1980' although the start of this period is unbounded. The aim of the present study was to understand the relationship between glass eel input and silver eel output with the specific objective of clarifying the context and the applicability of the Eel Regulation's 40% silver eel biomass escapement target. The fact that the Lough Neagh commercial eel metrics data set extends for ≈100 years allows this study to investigate any nonstationarity in conditions that influence eel production and the implications this might have for compliance with the Regulation.

2 | MATERIALS AND METHODS

2.1 | Study area

Lough Neagh is a large (385 km^2), shallow (mean depth 9 m), hypertrophic lake in Northern Ireland (Figure 1) with a long enrichment history (Foy *et al*., 2003; Wood, 1998). Its 4453 km^2 catchment is mostly grassland (67%) and rough grazing (10%). The catchment drains 40% of the land area of Northern Ireland, through six major rivers and a number of minor rivers. Potential barriers to eel migration within these rivers have been assessed as minimal and resident eel populations derived from electric-fishing surveys have shown them to be present but not abundant. Commercial eel fishing has never taken place in the affluent rivers and an examination of illegal fishing gear seizures also suggests that they are not targeted, indicating a low output of eels.

The Lough drains north to the Atlantic Ocean *via* the River Bann (38 km long). The estuary extends 9.7 km upstream from the mouth to The Cutts, where prior to the 1930s further tidal ingress was prevented by a natural fall and by three sluice gates post-1930s. The River Bann is a heavily regulated system designed to control the flow of water leaving Lough Neagh. Following the construction of the flood control and drainage scheme in the 1930s, the upstream migration of glass eel was impeded, the flow through the sluice gates being too strong for glass eels to swim against. To mitigate the impact, two elver traps are sited, one at either bank, consisting of ramps leading into concrete boxes supplied with a small flow (Rosell, 2002). Glass eels

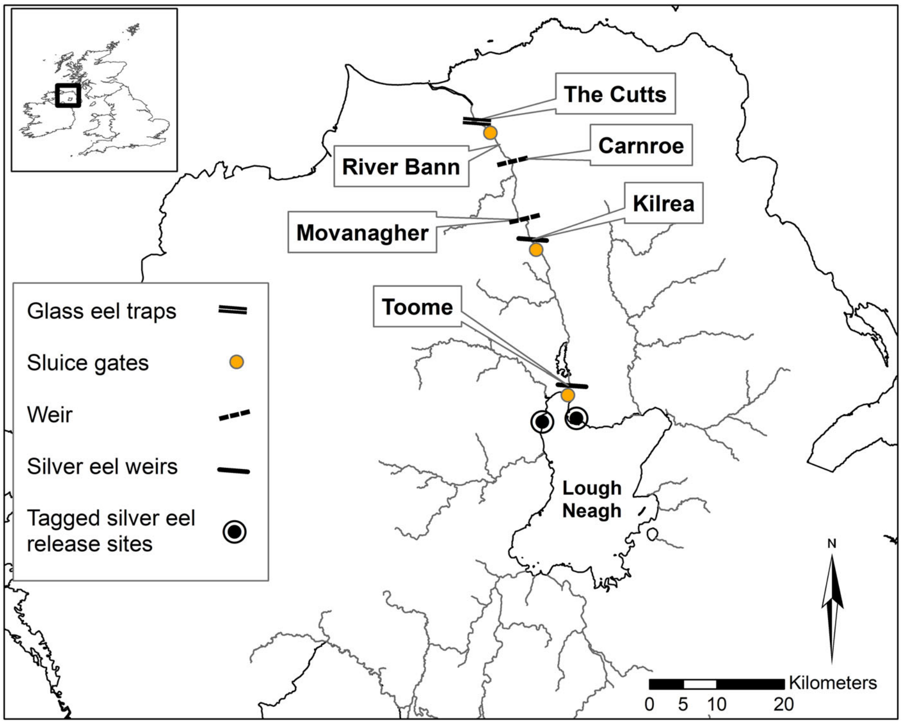


FIGURE 1 The study area showing the location of the glass eel traps at The Cutts and the silver eel weirs at Kilrea and Toome. The location of the silver eel release sites (circles), sluice gates (orange circles) and weirs (dashed line)

ascend the ramps into the boxes on straw ropes and are prevented from exiting upstream. The boxes are emptied into a tanker and the glass eels taken to Lough Neagh and released from the quaysides around the circumference of the lough on a daily basis during the period of their immigration phase. Trap and transport of glass eels prior to the 1930s was not in use, the flow patterns in the river being under natural conditions.

During the period 1949–1959, glass eels were not transported upstream into the lough. However, their upstream passage around the River Bann flood barriers was facilitated by emptying the elver traps into the river upstream of the sluice gates and fitting straw rope ladders through elver passes (Donnelly, 1986; B. Mc Elroy, personal communication). A proportion of glass eel recruits naturally circumvent the sluice gates (Kennedy & Vickers, 1993), but observation at elver passes upstream would suggest these are not significant quantities.

2.2 | Description of the fishery

The harvesting of eels as a food source in the Neagh-Bann system is a long-established activity as evidenced from food remains recovered from a 9000-year-old Mesolithic settlement at the Cutts (Waddell, 1998). A detailed description of the Lough Neagh eel fishery can be found in Donnelly (1986), Frost (1950), Rosell *et al*., (2005) and the Neagh-Bann Eel Management Plan (EMP) (Anonymous, 2010). The commercial harvest of eels began primarily as a silver eel fishery in the latter years of the 19th century with the yellow eel fishery developing later in the early part of the 20th century. The silver eel and yellow eel fisheries operated as separate entities until 1965 (Kennedy, 2000), since when the ownership of all the eel fishing rights have rested with the Lough Neagh Fishermen's Co-operative Society Ltd (LNFCS), who became the sole buyers of all eels caught.

Emigrating silver eels were caught in fixed Coghill nets lowered into the flow at two weirs on the River Bann, at Toome at the outlet of the Lough and at Kilrea 28 km downstream (Figure 1 and Supporting Information Photos S1 and S2). The mesh (knot to knot) in the silver eel nets tapers from 18 to 20 mm at the mouth to 6 mm in the cod end. The optimum fishing conditions differ for the two sites: Kilrea fishes best in the early part of the season at a flow of 20 m^3s^{-1} and Toome in late autumn/winter at 170 m^3s^{-1}. There have been significant changes in the structure and location of the weir at Toome, with the current structure and position operating since 1947 (Frost, 1950). Prior to 1947, photographs and drawings from the late 19th to the early 20th century showed that pre-1947 the Toome weir and the current weir at Kilrea were similarly constructed (Supporting Information Photo S3). The modifications and relocation from the edge of the lough (Supporting Information Photo S4) to the main river allowed it to fish more effectively at higher flows and extend the fishing season from August to the end of December. Previously the season would end in October as the old weir was inoperable during high flows through autumn and winter.

Silver eel migration is seasonal, with the majority leaving from early September to late December. The migration is primarily linked to flow and the onset of a new moon, and secondary to low pressure storm events bringing favourable southerly winds (Allen *et al*., 2006; Frost, 1950). This association is well known and fishing effort is targeted towards these conditions.

The yellow eel has been exploited by three main methods: longline, draft net and otter trawl. The use of otter trawls for the taking of eels began on a trial basis in 1960 but by 1963 had become established on a large scale with 50 out of 150 boats reporting using this method (Anonymous, 1965). The trawlers operated between May and October. Trawling ceased in 1973 and is currently not permitted by the LNFCS because of the risk of overexploitation, damage to the lough bed and its incompatibility with longline fishing on the same fishing grounds. The season runs from May to September. Longlines of 1200 hooks are fished overnight baited with earthworms (*Lumbricus* spp.), whole fish fry, pieces of fish flesh or more recently mealworms (various Coleopteran larvae available through the pet food trade). Draft nets 80–100 m in length with a 14 mm cod-end are deployed from a boat in open water. Changing market forces and the ageing fisher population has meant that boat numbers have decreased from about 200 in 1985 to around 80 in 2020 (LNFCS, personal communication).

Yellow eel fishery conservation measures include daily quotas (a cap on the weight of eels which the LNFCS will buy from any fisher, which can vary through the season from 38 to 50 kg boat^{-1} day^{-1}) and a 2 day weekend close period. The LNFCS applies a minimum marketable grading length for yellow eels of 400 mm, with any undersized eels returned to the water at their point of capture. Prior to that the legal minimum size was 300 mm and in the early part of the 20th century there was no lawful size limit (Menzies, 1924).

2.3 | Environmental data

Mean daily discharge for the River Bann (m^{3}s^{-1}) at Movanagher (Figure 1) and environmental data for Lough Neagh, water temperature (°C) at a depth of 10 m, total phosphorous and chlorophyll a were available from the late 1960s/early 1970s onwards. Pre-1971 levels in total phosphorus were extracted from Foy *et al.* (2003).

Information on daily rainfall (http://climate.arm.ac.uk/calibrated/rain/index.html) dating back to 1837 was available from the Armagh Observatory (Mark Bailey, personal communication) and was used to develop a model to estimate the lower River Bann mean monthly flow at Movanagher (m^{3}s^{-1}) back to 1905. Each of the abiotic monthly time series were not stationary, and so a seasonal ARIMA model (1, 0, 1) × (0, 1, 1)12 was applied to induce stationarity. The residuals, after applying the seasonal ARIMA model, were then assessed for significant cross-correlation between the residuals of the water and air temperature time series, and the residuals of the flow and rainfall time series. Removing autocorrelation and seasonal patterns within each time series, prior to cross-correlating, enabled greater sensitivity to identify significant lags as potential explanatory variables when developing the models. The cross-correlation analyses revealed a significant positive lag at time zero (0) between flow and rainfall time series. The rainfall (U) data were used as a potential explanatory variable for predicting flow (L) for the month (X_j) and year y (Table 1):

$$L_{jy} = X_j + 28.712(\pm 1.743) \times U_{jy} \quad r^2 = 0.70, \; P < 0.01 \tag{1}$$

TABLE 1 Regression parameter (X_j) estimates for mean monthly flow [Equation (1)]

Month($_j$)	Regression parameter (X_j)	Standard error
Jan	108.582	7.668
Feb	86.937	9.086
Mar	62.920	9.142
Apr	19.848	9.117
May	−4.088	9.162
Jun	−24.088	9.081
Jul	−28.768	9.082
Aug	−23.895	9.057
Sep	−8.329	9.065
Oct	4.483	9.087
Nov	59.586	9.058
Dec	85.383	9.064

2.4 | Ethical statement

The care and use of experimental animals, including the floy tagging of silver eels, complied with UK animal welfare laws, guidelines and policies as approved by the Department of Health (Northern Ireland) PPL 2820.

2.5 | Stock recruitment

The Beverton–Holt model (Beverton & Holt, 1957) and the Ricker model (Ricker, 1954) were used to examine the relationship between the number of glass eels entering the lough (stock) and the total output measured as the number of silver eels that could potentially have left the lough (recruits). The models were:

Beverton–Holt model

$$R_y = S_y / (\alpha S_y + \beta) \tag{2}$$

Ricker model

$$R_y = S_y \, e^{\alpha(1 - S_y/\beta)} \tag{3}$$

and were used to estimate the stock recruit parameters α and β. The goodness-of-fit for the models was assessed as 1 – SS_{Res}/SS_{Tot}.

2.6 | Parameter estimation

2.6.1 | Stock: glass eel input

The input of trapped glass eels (kg year^{-1}) from the Cutts (natural), glass eels which have migrated naturally into and up the Bann estuary, were available for 1933–1948 and 1960–2020. Additional purchased glass eel input (kg year^{-1}) from Britain and France was available for 1984 to 2020 (stocked). From 1960 onwards the catches of glass eels were accurately weighed. However, during the period 1933–1948 the glass eels were placed on to trays and each tray was assumed to hold a fixed weight. Mass was converted to numbers assuming 3000 glass eels kg^{-1}.

These data form part of the model used by the EIFAAC/ICES/GFCM Working Group on Eel (WGEEL), in the ICES Annual Stock Advice, to forecast glass eel recruitment (ICES, 2017). In this study the model was used in reverse to hind-cast (reconstruct) natural recruitment for Lough Neagh. The WGEEL recruitment index used is a reconstructed prediction using a generalized linear model (GLM) with a gamma distribution and a log link:glass eel $\sim$ year: area $+$ site, where glass eel is individual glass eel time series, year is a categorical variable, site is the site monitored for recruitment and area is either the continental North Sea or elsewhere in Europe. As there are only few series available before 1960, a simplified version of that model considering a unique trend for Europe (*i.e.* no area term in the revised model) glass eel $\sim$ year $+$ site was used to predict the glass eel stock from 2020 back to 1923 (Figure 2a; Supporting Information Figure S1), the limit set by the reference data.

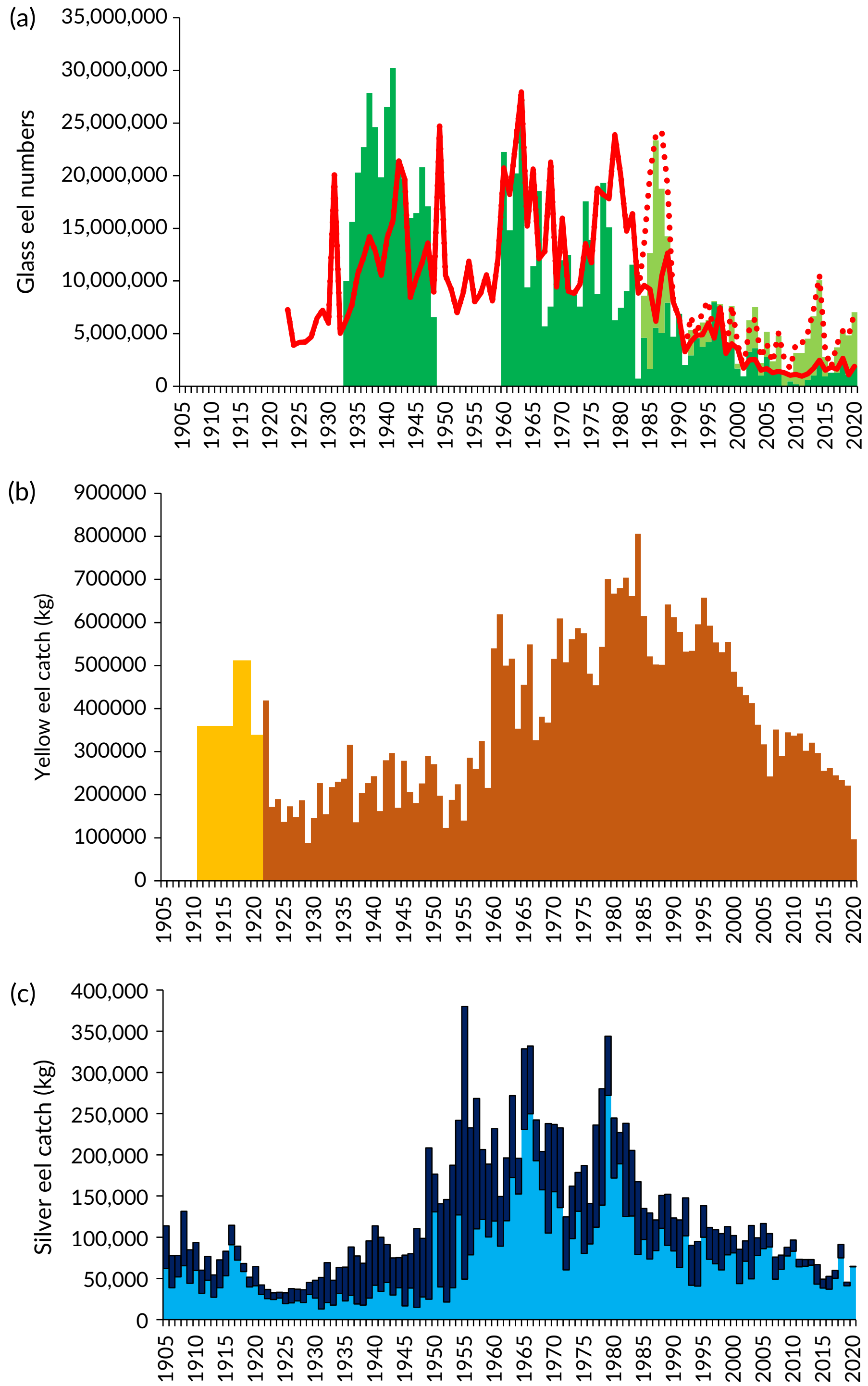


FIGURE 2 (a) Total input of glass eel from natural (green) and combined with stocked (light green). Reconstructed total number of glass eel recruitment from natural (red solid line) and with additional input from stocked (red dotted line) (numbers) from 1923 to 2020. (b) Yellow eel catch (catch estimated from Menzies (1924) (yellow) kg) from 1911 to 2020. (c) Annual time-series of silver eel catch (kg) at Toome weir (light blue) and at Kilrea (dark blue) from 1905 to 2020

2.6.2 | Recruits: silver eel output

There are three components to determining the total output: the catch of yellow eel which needs to be converted to silver eel equivalents (the number of silver eels that would have been expected to emigrate if the yellow eels had not been caught), the catch of silver eels and the quantity of silver eels emigrating pass the fishery.

Yellow eel

The annual declared catch (kg) data were available for yellow eel in the lough from 1922 to 2020. In addition, Menzies (1924) provides details of the mean catch of yellow eels per boat for a subsample (five boats) of the fleet, for triannual periods through 1911–1922, as well as the mean catch for 1922 and 1923. The mean catches for 1922 and 1923 were compared to the total reported catch for those years, which suggests that 159 and 145 boats were operating in 1922 and 1923, respectively. Assuming a fleet size of around 152 boats the mean catch per boat was used to estimate the total yellow eel catch for 1911–1921 (Figure 2b).

The yellow eel catch was converted to silver eel equivalents using data on eel size at age on capture, mortality estimates derived from the model of Bevacqua *et al.* (2011) and growth rates from (Aprahamian, 1988; Bark *et al.*, 2007; A. Walker, unpublished) to determine age-specific probabilities of silvering applied through the Scenario-based Model for Eel Populations (SMEPII) (Aprahamian *et al.*, 2007; Walker *et al.*, 2013) (Table 2).

Silver eel

Silver eel catch. The annual declared catch (kg) data were available for silver eel separately for each weir from 1905 to 2020 (Figure 2c).

Silver eel escapement. Male silver eels mature from 268 to 482 mm (mean 396.6 ± 4.1 mm, $n = 203$) and females from 424 to 983 mm (mean 609.6 ± 14.6 mm, $n = 200$). The 6 mm mesh size in the cod end would suggest the nets are not size selective (Bevacqua *et al.*, 2009). Silver eel escapement was quantified annually in 2003–2006 and 2007–2016 by mark recapture ($n = 12{,}098$ tagged silver eels). Over this period random samples of 145–320 emigrating silver eels which had been caught in the commercial fishery at Toome weir were tagged with FLOY™ tags and released the following day back into Lough Neagh at two open-water locations ≈8 and 10 km south from the weir (direct line). The number of batches released per year, during period of silver eel migration, ranged from 1 to 6 and batch release was timed to coincide with the new moon. The catch was processed the morning following capture and tags removed and classified according to weir of capture and batch. Underreporting of tags was tested by seeding batches of tagged fish at random into the catch and ranged from 0 to 2%. For every batch of tagged silver eels released back into the lough, control sets of 30 tagged and 30 untagged silver eels were placed in a large commercial holding cage lowered into the River Bann at Toome with their health status and longevity monitored daily over a 15-day period. Mortalities after 5 days were 1.45 and 0.08% for tagged and untagged fish and after 15 days 12.3% and 13.1%, respectively. There was no significant difference in the mortality rate between the two groups ($n = 960$, $P > 0.05$) over the 15 days. Tag loss per batch was less than 1% over the 15-day period.

TABLE 2 Mean length at age of female yellow eel caught in the fishery and the estimated proportion of an age group likely to emigrate as a silver eel

Age (years)	Mean length (mm)	Proportion estimated to emigrate as silver eel
7	414	0.5439
8	432	0.5887
9	449	0.6371
10	467	0.6895
11	485	0.7461
12	503	0.7682
13	521	0.8272
14	538	0.8754
15	556	0.9095
16	574	0.9197
17	592	0.9334
18	610	0.9523
19	628	0.9523
20	645	0.9523
21	663	0.9523
22	681	0.9523
23	699	0.9523

The exploitation rate (the number of tagged eels recovered in the catch/the total number of tagged eels released into the population) for each weir was correlated against flow on the day after tagging, as the majority of the fish were caught 1–3 days after tagging and because of the regulated system the coefficient of variation was low (≈0.10). For both weirs there was a significant relationship ($P < 0.05$) between the exploitation rate and flow (Supporting Information Figure S2) which could be best described by the equations [95% confidence intervals (CIs) in brackets]:

$$\text{Toome}\,(T): E_d^T = 4.157(1.594;10.844)L_d^{0.3602\,(0.161;0.56)}\quad r^2 = 0.378 \tag{4}$$

$$\text{Kilrea}\,(K): E_d^K = 18.681(8.864;39.373)e^{-0.021(-0.030;-0.017)}\,L_d\,r^2 = 0.608 \tag{5}$$

where $E_d^{T/K}$ is the exploitation rate for Toome (^{T}) or Kilrea (^{K})and L is flow (m^3s^{-1}) the day ($_d$) after tagging.

For the period 2003–2016 daily catches ($C_d^{silver_{T/K}}$), in number of females and males caught at either Toome (T) or Kilrea (K) weirs, were available and using the relationship between exploitation rate ($E_d^{T/K}$) and flow (L) (Equations 4 or 5), the total silver eel abundance for each day and for each weir could be calculated as $C_d^{silver_{T/K}} / E_d^{T/K}$. The two weirs fish in series, with Toome fishing first because it is closer to the lough, but in some instances both weirs were operating whereas on others only one or other of the weirs operated. The total output was estimated using the following criteria:

1. When Toome only was fishing the total silver eel output was estimated using the catch and the exploitation rate for the mean flow on that day was estimated using Equation (4) ($C_d^{silver_T} / E_d^T$).
2. When Kilrea only was fishing the total silver eel output was estimated using the catch and the exploitation rate for the mean flow on that day was estimated using Equation (5) ($C_d^{silver_K} / E_d^K$).
3. When both weirs were operating the estimate was based on which weir was predicted to have the higher exploitation rate on the day (catch efficiency at each weir is differently influenced by river flow conditions: Toome fishes better in high flows whereas Kilrea fishes better in low flows). If Toome was predicted to have the higher exploitation rate, then total silver eel output was estimated as above. If Kilrea was predicted to have the higher exploitation rate, then total silver eel output was estimated as above and any catch at Toome was added to the estimate, as these fish are effectively removed from the population before they reach Kilrea.

The total silver eel output (catch ($C_{yh}{}^{silver}$) plus escapement, the number of fish migrating past the fishery ($A_{yh}{}^{silver}$)) for the harvest year (y_h), was the sum of the daily estimates:

$$A_{y_h}^{silver} + C_{y_h}^{silver} = \begin{cases} \sum_{d=1}^{d=n} C_d^{silverT} / E_d^T & where : E_d^T \geq E_d^K \\ \sum_{d=1}^{d=n} C_d^{silverT} / \left(C_d^{silverK} / E_d^K\right) & where : E_d^K > E_d^T \end{cases} \quad (6)$$

The estimates of the total exploitation rate for the fishery and catch as a proportion of the total silver eel output taken by each weir has fluctuated over the period 2003–2016 (Table 3), with a mean (±95% CI) exploitation by the whole fishery of 25.0 ± 2.2%.

Silver eels migrate during the autumn, at night, mainly under periods of high flow (Frost, 1950). The overall exploitation rate (E^{silver}) increased with mean October–November flow (Supporting Information Figure S3) and can be described by the equation:

$$E^{silver} = 0.1943\,(\pm 0.0490) + 0.00052\,(\pm 0.00042)\overline{L_{10-11}}\; r^2 = 0.38, P < 0.02 \quad (7)$$

where:

$\overline{L_{10-11}}$ is mean October and November flow.

Equation (7) was used to estimate the exploitation rate for the period 1947 to 2002 and the observed exploitation rate for the years 2003–2020. The full exploitation *versus* flow data was not used as the basis to estimate the historic exploitation rate, as the aim was to develop population models and test their predictive capabilities against the observed 2017–2020 catch and escapement data (Aprahamian & Evans, in prep.). For escapement estimates prior to 1947, an informed judgement had to be made on the exploitation rate of the old (pre-1947) Toome weir. The old Toome weir was similar to the current weir at Kilrea and was likewise ineffective at fishing under high flows. It was therefore assumed that the old Toome weir would have had a similar exploitation rate to Kilrea of 6.1% (Table 3). A combined exploitation rate of 12.2% was therefore used to estimate total output for the period 1905–1947.

TABLE 3 The total exploitation rate for the whole fishery and the catch as a proportion of the total output taken by each weir between 2003 and 2016

Year	Whole fishery	Toome	Kilrea
2003	19.4%	8.0%	11.5%
2004	28.2%	20.9%	7.3%
2005	29.5%	20.9%	8.5%
2006	19.0%	15.6%	3.4%
2007	23.4%	14.1%	9.4%
2008	25.8%	19.1%	6.7%
2009	24.2%	20.6%	3.6%
2010	26.6%	22.9%	3.8%
2011	31.9%	27.2%	4.7%
2012	24.9%	22.3%	2.6%
2013	25.6%	23.1%	2.6%
2014	30.2%	19.0%	11.1%
2015	22.6%	17.0%	5.5%
2016	18.5%	13.4%	5.1%
Mean	25.0%	18.8%	6.1%
95% CI	2.2%	2.6%	1.6%

2.7 | Cohort data

Annual yellow and silver eel catch, and silver eel escapement data were converted to cohort data using information on the age profile and sex composition of the catch.

2.7.1 | Age profile of the fished eel population

Samples of eels were taken annually throughout the year from 2003 to 2017 to make up a sample representative of the whole yellow (n = 4650) and silver (n = 1400) fishing period. Length (mm), mass (g) and sex, following dissection to macroscopically identify gender, were recorded. A subsample from these eels (n = 3200) was aged from dried otoliths superglued to glass microscope slides, progressively ground using a gradation of fine emery papers to a surface through the origin and outer otolith edge, and read by transmitted light on a binocular microscope (ICES, 2009a). The age profiles (Anonymous, 2010) indicate that male silver eels start to mature at age 5 and almost all have silvered by age 11, whereas females mature from age 10, reaching a peak at 17 years old, with a maximum of 28 years (Anonymous, 2010; Supporting Information Figure S4]. The size limit (≥400 mm) in the yellow eel fishery has the effect that yellow eels start contributing to the fishery from age 7, reaching a peak at age 11–14 years (Anonymous, 2010). Data are also available for previous years (Anonymous, 1965; Frost, 1950), but the methodology used at that time has been questioned (Anonymous, 1966) and therefore we chose not to use these older data.

2.7.2 | Sex profile of the fished eel population

The sex ratio of the silver catch from 1922 to 1966 is reported in Anonymous (1966), with additional data during that period for the years 1943 and 1944 (Frost, 1950) and 1956 and 1957 (Jones, unpublished, cited by Anonymous, 1966). For the years 1965–1974 the sex ratios have been published in Parsons *et al*. (1977) and from 1975 to 1978 in Kennedy and Vickers (1993). From 2004 to present the sex ratios were based on macroscopic examination of a sample of 100 fish. For the period 1996–2016 the sex ratio data were available from annual UK Country Reports submitted to ICES (2007, 2009b, 2017) and were used to estimate the number per age group in the silver eel population ($C^{silver}_{a,y}$ and $A^{silver}_{a,y}$) post-1995. The studies other than that of Anonymous (1966) reported that gender was determined from macroscopic gender differentiation based on dissection. Anonymous (1966) is likely to have used size to identify sex (Frost, 1950; Parsons *et al*., 1977), the dimorphism shown is a reasonable surrogate for internal examination. To test the accuracy of this method surveys of catches which had been separated into small (male) and large (female) eels by the fishermen were gender determined macroscopically following dissection. Samples were based on an annual sample of 15 kg of eels between 2003 and 2019. Those classified as small were 97.2% male and those as large were 98.6% female. The data has been taken to be representative of the population as the design and operation of the Coghill nets have remained unchanged and it has been assumed that the sampling programme was statistically robust.

Parsons *et al*. (1977) and Geffroy and Bardonnet (2016) have shown a density-dependent relationship between sex ratio and abundance with an increase in the proportion of males in the silver eel population with increasing stock density. Taking the silver eel catch as an index of the abundance of the stock, there is a significant relationship between the silver eel catch in harvest year y_h and the sex ratio (proportion males) in the silver eel catch 8 years later, $y_h + 8$ (Supporting Information Figure S5). The relationship can be described by:

$$r_{y_h+8} = 0.2163(\pm 0.073)\ln C^{silver}_{y_h} - 2.122(\pm 0.852)\ r^2 = 0.34;\ P < 0.001 \quad (8)$$

where r_{yh+8} is the sex ratio measured as the proportion of males in the silver eel catch in year $y_h + 8$ and C^{silver}_{yh} is the catch of silver eels in year y_h.

The sex ratio of yellow eels ≥400 mm was 96.4% female ($n = 979$), the remainder being undifferentiated, and was based on macroscopic examination following dissection (Anonymous, 2010). For the purpose of this model the yellow eel catch was assumed to be 100% female.

2.7.3 | Mass profile of the fished eel population

Estimates of the mean length and mass of female and male silver eels caught in the silver eel fisheries are available for a number of years: 1943 and 1944–1946 (Frost, 1950), 1956 (Jones, unpublished) and 1971–1974 (Parsons *et al*., 1977). Since 1996 the total catch has been graded into large (female) and small (male) eels of mean mass 367 ± 18 g and 125 ± 3 g, respectively (LNFCS, unpublished). The mean mass of yellow eels in the catch was 308 ± 9 g (ICES, 2007, 2017).

2.7.4 | Uncertainty

Monte Carlo simulation (100 iterations) was used to address uncertainty in the parameter estimates and to calculate confidence intervals.

2.8 | Total silver eel output

Recruitment (total silver eel output) (R_y) estimates (for each cohort y) were the sum of the number of silver eels emigrating past the fishery $\left[\sum_{a=5}^{28} A^{silver}_{y_h,a,s}\right]$, the catch of silver eels $\left[\sum_{a=5}^{28} C^{silver}_{y_h,a,s}\right]$ and the catch of yellow eels converted to silver eel equivalents by multiplying the number of yellow eels of age a by the age specific value in Table 2, $\left[\sum_{a=7}^{23} C^{yellow}_{y_h,a} v^{silver}_a\right]$, as follows:

$$R_y = \sum_s \left(\sum_{a=5}^{28} A^{silver}_{y_h,a,s} + \sum_{a=5}^{28} C^{silver}_{y_h,a,s} \right) + \sum_{a=7}^{23} C^{yellow}_{y_h,a} v^{silver}_a \quad (9)$$

where $A^{silver}_{y_h,a,s}$ represents the escapement of silver eels (in numbers), $C^{silver}_{y_{h,a,s}}$ represents the catch (in numbers) of silver eels from the silver eel fishery from harvest year y_h for sex s (= *female* or *male*), $C^{yellow}_{y_{h,a}}$ the catch of yellow eels (in numbers) from the yellow eel fishery from harvest year y_h, and v^{silver}_a the proportion of yellow eels of age a likely to emigrate as a silver eels (Table 2).

Furthermore, $C^{yellow}_{y_h}$ is derived from the yellow eel catch ($O^{yellow}_{y_h}$, in biomass) as follows:

$$C^{yellow}_{y_h} = O^{yellow}_{y_h} / w^{yellow} \quad (10)$$

where w^{yellow} is the mean mass of yellow eels in the catch and $C^{silver}_{y_h,s}$ is the silver eel catch ($O^{silver}_{y_h}$, in biomass) and exploitation rate in the whole fishery ($E^{silver}_{y_h}$, as set out in section 2.6.2) as follows:

$$C^{silver}_{y_h,s} = \frac{O^{silver}_{y_h} E^{silver}_{y_h}}{w^{silver}_{male} r_{y_h} + w^{silver}_{female}(1 - r_{y_h})} \quad (11)$$

and

$$A^{silver}_{y_h,s} = \frac{O^{silver}_{y_h} E^{silver}_{y_h}}{w^{silver}_{male} r_{y_h} + w^{silver}_{female}(1 - r_{y_h})} \quad (12)$$

where w^{silver}_s is the mean mass of silver eels of sex s (*female* or *male*) in the catch and r_{y_h}, the sex ratio for males in year y_h, is calculated as follows [using Equation (8)]:

$$r_{y_h} = \begin{cases} \overline{r_{y_{1913-1918}}} & y_h < 1913 \\ 0.2163\ \ln\left(O^{silver}_{y_h-8}\right) - 2.1215 & y_h \geq 1913 \end{cases} \quad (13)$$

2.9 | Natural mortality

The estimation of instantaneous annual natural mortality rate (M) was based on the assumption that by age 29 all eels had been caught, emigrated or died (Supporting Information Figure S4), and was assumed to be constant throughout the eel's lifespan. For each cohort estimates of the number of glass eels and age-specific estimates of the number of yellow and silver eels caught and the number of silver eels escaping the fishery were available.

The instantaneous annual natural mortality rate, from the glass eel stage onwards, was calculated by iteration for each cohort from 1923 to 1994. Equation (14) assumes a constant annual mortality and takes the initial glass eel input together with the age-specific losses from catch and emigration to estimate age-specific abundances. M is the value that minimizes the number of eels alive after 28 years (*i.e.* $N_{29} \approx 0$);

$$N_{29} = N_{a=0,y} e^{-29M}{}_{y} - \sum_{a=1}^{29} \left(C_{a,y}^{yellow} - C_{a,y}^{silver} - A_{a,y}^{silver} \right) e^{-(a-1)M}{}_{y} = 0 \quad (14)$$

where $N_{a,y}$ is the number of fish alive of age a, cohort y at the start of the year.

3 | RESULTS

3.1 | Total output

The estimated total output: yellow eel catch as silver eel equivalents, catch of silver eel plus silver eel escapement, for the years 1905–2020 shows a period of high output from the 1950s to the mid-1980s, with a peak output of 1975 t in 1979 but declining steadily since the mid-1980s (Figure 3). At its peak Lough Neagh was producing annually between 35 and 45 kg ha^{-1} year^{-1} (Figure 3) but this has fallen to 10–15 kg ha^{-1} year^{-1} in recent years.

There is some uncertainty on the level of total output for the period 1905–1922. At the start of the time period, output may be underestimated as no yellow eel catch was declared for the period 1905–1922. This may reflect either an underdeclaration and/or the fact that the fishery was predominantly based on silver eels at that time. The method used to estimate the catch between 1911–1921 may have overestimated the yellow eel catch. It was assumed that the catch from five boats was representative of the fleet of ≈150 boats. Catch is known to vary among fishermen, with some individuals catching more than others (Hilborn, 1985). If that was the case then the predicted output would be inflated. This would seem likely as the estimated catch between 1911 and 1921 was markedly higher than that declared in subsequent years (Figure 3).

3.2 | Stock recruitment relationship

3.2.1 | Glass eel stock

The model underestimated the catches of glass eels between 1933 and 1948 ($r^2 = 0.33$, $P < 0.02$) and overestimated the catch between 1979 and 1988 ($r^2 = 0.27$, $P > 0.05$), but in general, post–1960 ($r^2 = 0.66$, $P < 0.001$), the reported recruitment values are consistent with the common index (Supporting Information Figure S6). Overall, the model explained 50.7% of the variability ($P < 0.001$). The underestimate between 1933 and 1948 may reflect (a) that the method used to quantify the River Bann count was less accurate when compared to that post–1960 and/or (b) that there is a historical bias in some of the longest historical series built on total catch of fisheries which changed over the period 1960–1979 when glass eel fishing became more commercialized. During the period pre-1960, the limited dataset available makes the historical trend even more uncertain.

The model prediction and that observed (Figure 2a) showed that for the years 1949–1959 the predicted glass eel stock was lower than that observed between 1933 and 1948 and from 1960 to 1979 but

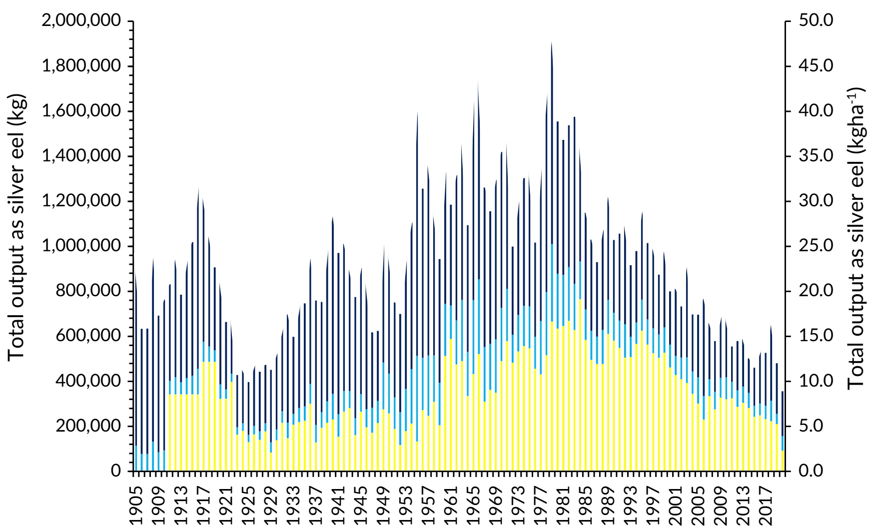


FIGURE 3 Total output (kg year^{-1}) yellow eel catch as silver eel equivalents (yellow), silver eel catch (light blue), silver eel escapement (dark blue) and total annual production (kg ha^{-1} year^{-1}) for calendar years 1905–2020

these lower catches are reflected by the Bann glass eel abundance series, which decreased from 1941 to 1948.

3.2.2 | Stock: recruitment

The reconstructed glass eel data were used to examine the relationship between stock and recruitment. There was no significant difference ($P > 0.05$) between the coefficients of the Beverton–Holt stock recruitment relationship modelled using the observed data and that extrapolated using the WGEEL index in those years where counts of glass eels were available (1933–1948, 1960–1997) (Supporting Information Figure S7). The Ricker model did not produce a valid output. The goodness-of-fit test generated a negative number indicating a poor fit to the data; effectively the model fit was worse than using the mean value.

The relationship between the glass eel stock from 1923 to 1997 and the number of silver eel recruits can be described by Beverton–Holt and by Ricker stock recruitment relationships (Figure 4). The 1923–1994 cohorts will have been fully recruited by 2020 (Anonymous, 2010) and the data for the 1995–1997 cohorts have been included as they represent >95% of the total output by 2020. The Beverton–Holt model shows that silver eel output increases with increasing numbers of glass eels entering the lough, reaching a plateau of 3.75–4.0 M silver eels beyond which no further silver eels are produced. The Ricker model indicates a maximum output at 4.2 M silver eels at an input of 15.9 M glass eels.

The relationships (with 95% CIs) are described by the equations:

Beverton–Holt

$$R_y = S_y / \left(2.248.10^{-7}(1.804.10^{-7} : 2.740.10^{-7}) S_y + 0.596\,(0.095 : 1.154)\right) \tag{15}$$

Ricker

$$R_y = S_y\, e^{-0.336\,(-0.140:-0.533)\left(1-\frac{S_y}{-5.36}*10^6\right)\,(-2.62.10^6:-7.44.10^6)} \tag{16}$$

There is some suggestion indicated in Figure 4 that the carrying capacity of Lough Neagh has changed over the last century. There was a period of low productivity during the early part of the time series affecting the 1923–1943 classes. This was followed by a period of high productivity impacting on the 1944–1975 classes followed by a decline in productivity which has persisted until today.

The data were partitioned pragmatically according to whether or not the years were above the mean value of silver eel recruits (3.77×10^6). The responses to a presumed change in the ecology of Lough Neagh took place over a 6-year period. Silver eel output (recruits) for a given level of glass eel stock increased from ≈3.25 million individuals (≈1,000,000 kg) for the 1923–1943 cohorts before stabilizing at the higher productivity level of ≈5.0 million individuals (≈1,550,000 kg) for the 1948–1971 cohorts. Output then declined steadily for the 1972–1975 cohorts before settling at the lower level of ≈3.25 million individuals (≈1,000,000 kg) for the 1976–1997 cohorts (Figure 4). The model indicates that maximum output is achieved with an input of around 11,500,000 glass eels (300 ind ha^{-1}).

The relationships for the Beverton–Holt model for the two ecological states and associated time periods (Figure 5) were:

High productivity: 1944–1975

$$R_y = S_y / \left(1.87.10^{-7}(1.63.10^{-7} : 2.10.10^{-7}) S_y + 0.29(0.04 : 0.59)\right) \tag{17}$$

Low productivity: 1923–1943 and 1976–1994

$$R_y = S_y / \left(2.77.10^{-7}(2.34.10^{-7} : 3.19.10^{-7}) S_y + 0.58(0.19 : 0.99)\right) \tag{18}$$

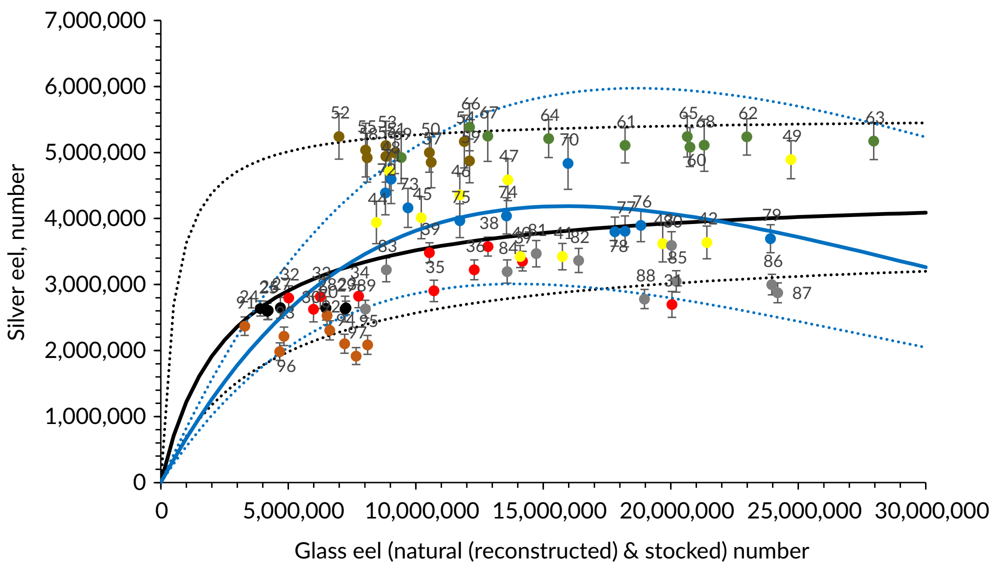
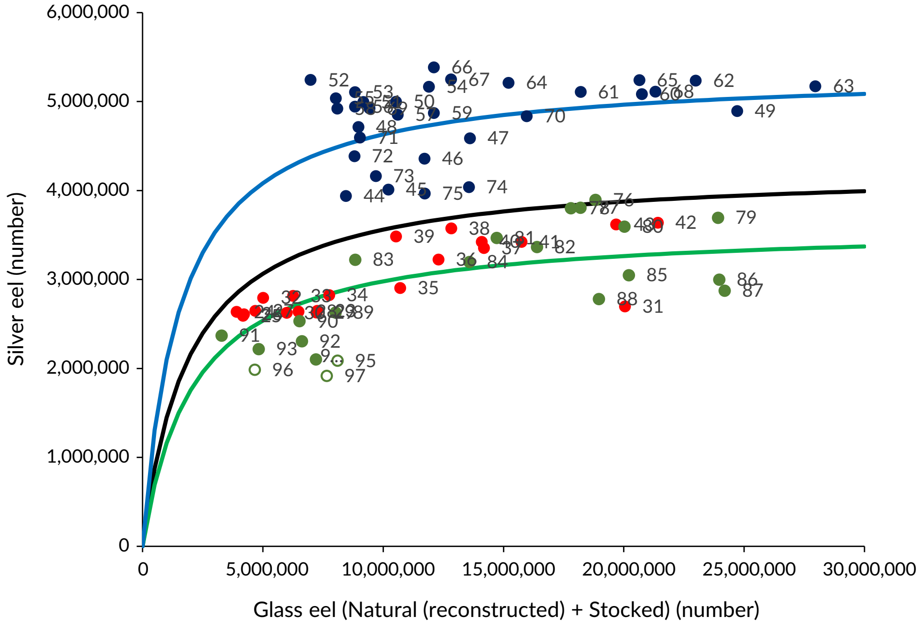


FIGURE 4 Beverton–Holt (black lines) and Ricker (blue lines) relationships between recruits (silver eel) and stock (glass eel) for the glass eel cohorts 1923–1997, with 95% confidence limits (dotted lines). Error bars indicate 95% confidence intervals. Numbers refer to glass eel cohort years, colours to decades: 1920s (black), 1930s (red), 1940s (yellow), 1950s (brown), 1960s (green), 1970s (blue), 1980s (grey), 1990s (orange)

FIGURE 5 Beverton–Holt relationship between recruits (silver eel) and stock (glass eel) for the glass eel cohorts 1923–1997 (black), 1944–1975 (blue), and 1923–1943 and 1976–1994 (green). Numbers refer to glass eel cohort years. Open circles indicate cohorts where silver eel output is >95% R_y < 100%



The Ricker model did not produce a valid output for the two states.

3.3 | Natural mortality

The annual instantaneous rate of natural mortality increased with the density of glass eels stocked into Lough Neagh (Figure 6). The mortality rate ranged from a low of 0.017 year^{-1} at densities of 100–200 glass eels per hectare to a high of 0.108–0.142 year^{-1} at densities of 600–700 glass eels per hectare, with a mean rate of 0.073 ± 0.007 year^{-1}. Over the time period (Figure 7a) the mortality rate increased significantly by 0.00054 ± 0.00033 year^{-1} (r^2 = 0.12, P = 0.002). To account for the effect of glass eel density (Figure 6), the natural mortality rate was standardized to the mean stocking density over the period (339 glass eels per hectare). The analysis (Figure 7b) shows that the natural mortality rate was fairly high for the 1923 to the early 1940s cohorts and then started to decline. It then stayed relatively stable before increasing again for the post-1970 cohorts. The rate for the 1944–1975 cohorts was approximately 0.02 year^{-1} lower when compared with those between 1923 and 1943 as well as from 1976 to 1994.

4 | DISCUSSION

The present study has relied heavily on the glass eel model developed by WGEEL to forecast abundance (ICES, 2017), but used here to hindcast the glass eel stock up to 1923. The values predicted by the model are low for the period 1949–1959, consistent with the Bann series, which decreased between 1941 and 1948. Since the prediction is based only on results available from two to six data series during that time, there is the risk that the 'common trend' predicted is driven by local factors acting on those time series rather than a general, whole-stock trend. However, the series consistently reported low values before a significant increase at the beginning of the 1960s, suggesting that abundance was low during this period. Post-1960, the model provided a good approximation to the observed count of glass eels post-1960 (Figure 2a), where more data sets are available.

The use of the reconstructed time series data has provided clarity on the changes in the dynamics of the stock and the ecological changes within the lough. It would not have been possible using only the observed data because of their discontinuity (Figure 2a). The observed data do, however, represent a minimum estimate as an unknown proportion of the glass eel stock circumvents the weir (Kennedy & Vickers, 1993). This proportion is likely to be greater when glass eels are more abundant. The upriver movement of eels, past the Cutts and upstream through the river, is likely to be driven by density-dependent pressures (Briand *et al.*, 2005; Feunteun *et al.*, 2003; Ibbotson *et al.*, 2002; Smogor *et al.*, 1995). This suggests that the stock of glass eels migrating into the lough during the period 1949–1959 was at a high enough level and that the mitigation measures in place at the time adequate such that the output was not measurably impacted (Figure 4). Conversely, following the decline in the glass eel stock post-1983, the density-dependent pressure driving upstream migration will have been reduced. As a consequence, the catches of glass eels from the Cutts may be a more accurate reflection of abundance.

4.1 | Limitations of the study

The present study used a single age structure to describe the yellow and silver eel populations throughout the time period (Anonymous, 2010). Although historic information on the age profile of the eel population was available (Anonymous, 1965; Frost, 1950),

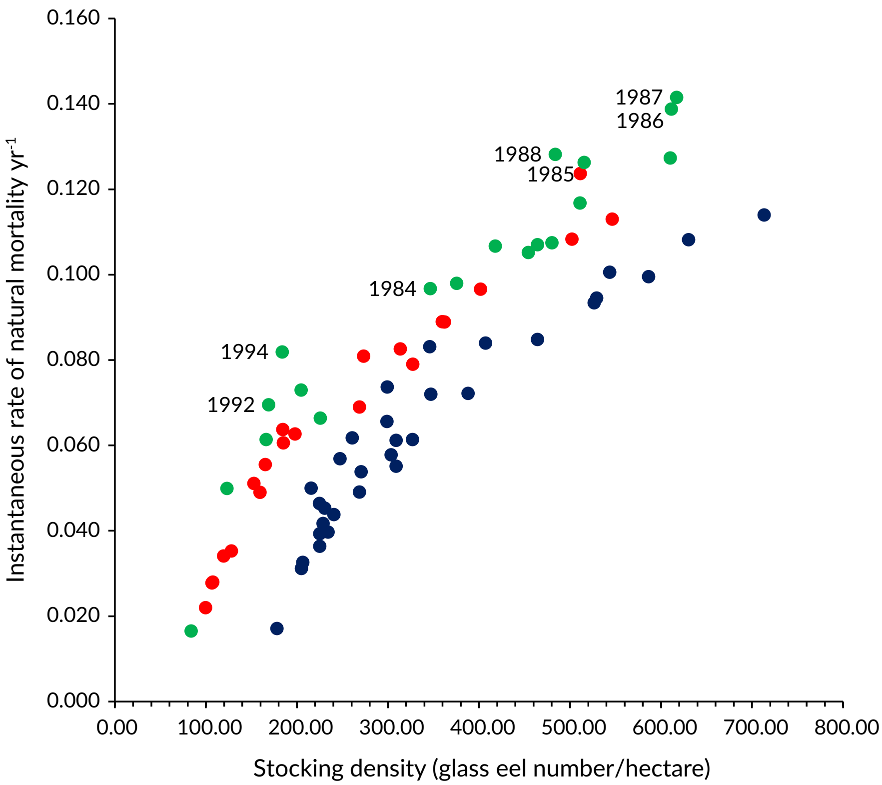


FIGURE 6 Annual instantaneous natural mortality in relation to the stocking density of glass eel for the 1923–1943 cohorts (red), 1944–1975 (blue) and 1976–1994 (green). The stocked years **1984–1994 are highlighted**

the method used has since been invalidated (ICES, 2009a) and thus the information was not used in this study. Silvering is more dependent on size than it is on age (Vøllestad, 1992). A constant age structure may be invalid if growth rate is density-dependent (De Leo & Gatto, 1995), which would seem likely, in the same way as natural mortality was shown to be density-dependent (Figure 6).

The age profile of the yellow eel catch (Anonymous, 2010) is a direct consequence of the 400 mm size limit, which was applied from at least 1965 (Anonymous, 1965). Prior to that the legal minimum size was 300 mm and in the early part of the 20th century there was no lawful size limit (Menzies, 1924). The effect of a lower size limit and the absence of knowledge on the size/age structure of the yellow eel catch has meant that the age structure published in Anonymous (2010) has been taken as the *de facto* age structure. This is considered valid, assuming a constant growth rate, as the market set the effective size limit, a 400 mm eel being the smallest size for smoking. It was only later (1965) that the regulatory authority formalized the status quo.

The estimate of the sex ratio was based on the size of the silver eel catch, taken as a surrogate for stock density. The preferred explanatory variable would have been the standing stock. To calculate the standing stock, information was first needed on the sex ratio to estimate numbers per age group. The relationship between sex ratio and silver eel catch in the previous 8 years [Equation (8)] indicates a higher proportion of males with increasing stock density. This is in agreement with the literature (Geffroy & Bardonnet, 2016). The data, with the exception of Parsons *et al*. (1977), used to estimate sex ratio was taken at face value and no details on the sampling strategy were available to make a judgement on its robustness. There is uncertainty in the validity of some of the data, especially as in some of the early records it was recorded that zero males emigrated.

This study also had to make an assumption on the level of exploitation in the silver eel fishery prior to 1947, when the current silver eel fishing weir was constructed at Toome. The assessment that the exploitation rate at Toome weir was the same as that currently operating at Kilrea was based on the analysis of photographs taken in the early 20th century. The photographs show that the weirs were similarly constructed, and it was apparent that (as is currently the case at Kilrea) they would not fish as effectively at high flows in comparison with the current weir at Toome. This also provides some evidence to explain why the old silver eel catch data tended to end in October as the old weirs were inoperable during autumn rains and subsequent high flows throughout autumn and winter. The new more robust, high-flow operable weir in 1947 would have started to impact on the output from the 1919 glass eel year class with increasing effect up until the 1942 year class. All following year classes would have been similarly affected.

The conclusion from this study that the total output for the 1923–1943 cohorts was lower than for those between 1944 and 1975 has been based, in part, on an exploitation rate pre-1947 of ≈12%. If output was to have been at the same level, then the exploitation rate would need to have been ≈6% during the first half of the 20th century. This would seem very unlikely as it would represent the exploitation rate of Kilrea weir on its own, no account being taken of the fishery at Toome weir. There is the possibility that the pre-1947 Toome weir was more effective and had a higher exploitation rate than the ≈6% assumed, but it is unlikely to have been similar to

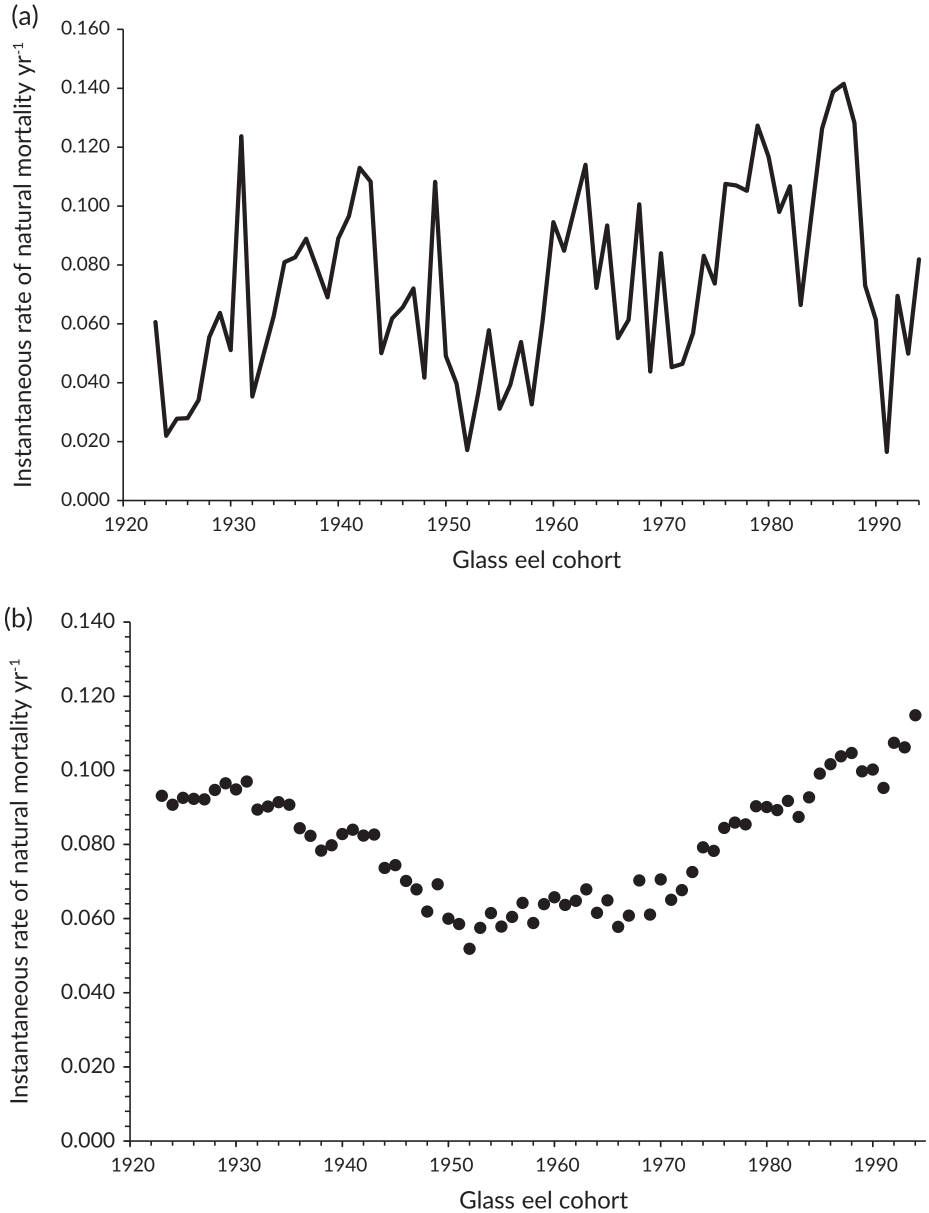


FIGURE 7 Trend in annual instantaneous natural mortality (a) and after standardizing to an average stocking density of 339 glass eel per hectare (b) for the 1923–1994 cohorts

current levels (Table 3; 25.0%) as the weirs at that time were not able to operate under high flows. The effect of a higher exploitation rate would be to further reduce the total output for pre-1942 year classes, supporting the conclusion that the productive capacity was lower during the early part of the 20th century.

The surface area of the lake, 385 km^2 (Wood, 1998), is assumed to have remained the same from 1905 to the present. However, a range of drainage schemes under the provisions of the Shepherd Scheme (in 1942), the Drainage Act (NI) 1928 (in 1959) and the Lough Neagh and Lower Bann Drainage and Navigation Act (NI) 1955 have lowered the average water level of the lough by 1.26 m (Carter, 1993), reducing the surface area by 3.6% from 399 (Lewis, 1837) to 385 km^2. If the marginal areas, those areas that are under water for a period of the year, are included, then the loss of feeding habitat estimated in 1956 (J.W. Jones, unpublished) would be 10.0%, a reduction from 438 to 398 km^2. Thus, the estimates of total output and yield, in terms of kg ha^{-1}, prior to 1959 are likely to have been overestimated by between 3.6 and 10.0%.

4.2 | Total output

The estimated total output (catch of silver eels, yellow eels as silver equivalents and escapement) for the period 1905 to 2020 (Figure 3) is similar to the trend in European landings and taken to be a surrogate for the size of the continental stock (Dekker, 2003). Although there is some uncertainty regarding total output (Section 3.1), the Lough Neagh stock was low in the early years of the 20th century, increasing from 1910 to the late 1910s before declining until the 1930s (Figure 3). It then increased steadily until the 1940s before declining again during the period 1940–1945. This decline was, however, more substantial for the continental stock compared to Lough Neagh and

TABLE 4 Total output of silver eel from lakes/lagoon systems across Europe

Lagoon/lake	Country	Silver eel production (kg ha^{-1} year^{-1})	Year	Reference
Bages Sigean Lagoon	France	30.00 60.00	2007 Pristine	Amilhat *et al*. (2008)
Camargue lagoon	France	25.00	2007	Bevacqua *et al*. (2007)
Comacchio lagoon	Italy	20.00 >14.00 6.15 11.8 ± 8.6 0.68 ± 0.36 30–35 (peak)	Pre-1979 1972–1975 1977–1991 1960–1997 1998–2013 1781–2013	Rossi (1979) De Leo and Gatto (1995) Aschonitis *et al*. (2015) Aschonitis *et al*. (2017)
Corrib	Ireland	3.57 1.70	1976–1982 2000–2007	Anonymous (2008)
Ennell	Ireland	2.7	2001–2007	Anonymous (2008)
Erne	Ireland	4.5	1955–1982	Anonymous (2008)
Erne	Ireland	1.62–1.70[a]	2010–2011	McCarthy *et al*. (2014)
Ichkeul Lake	Tunisia	19.1–29.2[a] 42.6	2013 Pristine	Derouiche *et al*. (2016)
Ijsselmeer	Netherlands	1.32–2.47[a] 16.4 (peak)	1989–1996 Late 1940s	Dekker (2000)
Or lagoon	France	13.20	2009	Charrier *et al*. (2012)
Porto Pino Lagoon	Sardinia, Italy	16.90	1979–1981	Rossi and Cannas (1984)
Shannon Lakes	Ireland	4.20	1992–1994	McCarthy *et al*. (1994)
Mediterranean basin	Various	≈20	Pristine	Aalto *et al*. (2016)

[a]Minimum and maximum reported silver eel production (kg ha^{-1} year^{-1}).

may reflect reduced effort (during WWII). Both time series then increased. The continental stock peaked during the late 1960s/early 1970s, whereas the Lough Neagh peak occurred later during the late 1970s/early 1980s, after which time both series declined. The earlier decline in the continental stock compared to Lough Neagh may relate to local issues, particularly the enrichment of the lough, which escalated during the 1960s (Foy *et al*., 2003).

Lough Neagh showed a period of high output from the 1950s to the mid-1980s, with an estimated peak output of ≈2000 t in 1979 (Figure 3). This can be compared with two other major enclosed systems, the Ijsselmeer and Comacchio Lagoon, where peak annual yields were 4750 and ≈1400 t, respectively (Aschonitis *et al*., 2017; Dekker, 2000). There is little escapement of silver eel in both cases, thus yield is virtually equivalent to total output. Comparison with other systems across Europe (Tables 4 and 5) indicate that at its peak Lough Neagh was one of the most productive environments for eels, comparable with the output from the Mediterranean lagoons. There are higher estimates for silver eel output, notably from France, but there are concerns over the assumptions made in the methodology (ICES, 2018).

The high level of output may relate to the high number of glass eels entering the lough, but the evidence from the stock recruitment analysis is that higher glass eel numbers did not result in a high silver eel output. Instead, the stock recruitment analysis suggests that there has been a regime shift within the lough. The estimates of carrying capacity [≈1000 t (1923–1943 and 1976–1997 cohorts) – ≈1550 t (1948–1971 cohorts)] are substantially lower than those calculated by Bevacqua and De Leo (2006) of 5000 t for Lough Neagh using the DemCam model and higher than those reported in the Neagh-Bann Eel Management Plan of between 400 and 600 t (Anonymous, 2010).

The increase in carrying capacity may be attributed to the increase in eutrophication of the lough, which was gradual until *c*.1960 after which nutrient levels increased very rapidly (Batterbee, 1978; Bunting *et al*., 2007; Carter, 1977; Foy *et al*., 2003), fuelled by the rapid rise in nitrogen (Bunting *et al*., 2007) and phosphorus (Foy *et al*., 2003; Supporting Information Figure S8). The elevated nutrient concentration will have enhanced algal production and Bunting *et al*. (2007) estimated that alga abundance had increased three-fold over the 60 years from the 1930s to the 1990s. Algae, and diatoms in particular, are a key component of the diet of chironomid larvae (Pinder, 1986). This increase in primary productivity is likely to have accounted for the dramatic growth in the chironomid population, which in turn increased ≈5–6 fold between the 1920s–1950s and the 1960s–1970s (Carter, 1977). Recent estimates (2010–2016) (Allen *et al*., 2016; Tománková *et al*., 2014) are considered higher than those of the late 1950s (H.B.N. Hynes, unpublished) and similar to those of 1969/1970 (Carter, 1977) and the late 1980s (Winfield, 1991), with larval densities substantially higher during the late 1990s (Bigsby, 2000) (Supporting Information Table S1). Chironomids are an important food source for eels (Frost, 1946; Marrion, 1986; Matthews *et al*., 2001; Moriarty, 1978), whilst Anonymous (1966) found the diet of eel in Lough Neagh was dominated primarily by chironomids and

TABLE 5 Total output of silver eel from open systems across Europe

River	Country	Silver eel production (kg ha^{-1} year^{-1})	Year	Reference
Brede aa	Denmark	49.00	1981	Nielsen (1982)
Burrishoole	Ireland	0.8–1.5[a] (5 years mean)	1970–2015	Poole *et al*. (1990, 2018)
Deba	Spain	6.10	2009	Diputación de Gipuzkoa & EKOLUR[b] (personal communication)
Elbe	Germany	0.84	2005–2007	IfB[c] Potsdam-Sacrow (personal communication)
Frémur	France	40–50[a] 17–42[a]	1996–1997 2000–2002	Feunteun *et al*. (2000) Acou *et al*. (2009)
Garavogue	Ireland	5.39	1962–1975	Anonymous (2008)
Huntspill	UK	6.00	2009	Bilotta *et al*. (2011)
Imsa	Norway	2.02 1.13	1975–1987 2010–2015	Vøllestad and Jonsson (1988) Poole *et al*. (2018)
Leaden	UK	0.94	2009	J. Hateley (personal communication)
Leven	UK	0.26 0.32 0.16	1942–1944 1994–1995 2000–2007	Lowe (1952) Knights *et al*. (2001) Aprahamian (personal communication)
Loire	France	16.36	2001–2005	Eric Feunteun (personal communication)
Moy	Ireland	5.52	1942–1952	Anonymous (2008)
Oir	France	4.8–6.9[a] 13.19	2000–2002 2009–2010	Acou *et al*. (2009) Charrier *et al*. (2012)
Oria	Spain	14.00	2009	Diputación de Gipuzkoa & EKOLUR[b] (personal communication)
Rhine	Germany	0.032–0.097[a]	2004–2005	Breteler *et al*. (2007)
Schwentine	Germany	0.06–0.13[a] 1.5–3.8[a]	2009–2010 Pristine	Prigge *et al*. (2013)
Shannon	Ireland	2.0 1.35–1.62[a]	2001–2007 2008–2011	Anonymous (2008) MacNamara and McCarthy (2014)
Stour	UK	2.36	2009	Aprahamian (personal communication)

[a]Minimum and maximum reported silver eel production (kg ha^{-1} year^{-1}).
[b]EKOLUR Asesoría Ambiental SLL.
[c]Department of Inland Fisheries (IfB).

Asellus spp., an observation reaffirmed during the long-term dietary analyses associated with this current study (D. Evans, unpublished). The enrichment would have also enhanced the phyto- and zooplankton production (Bunting *et al*., 2007; Wood & Smith, 1993), another benefit to the eel population.

The start of the rapid rise in 1960 of the lough enrichment (Bunting *et al*., 2007; Carter, 1977; Foy *et al*., 2003) and the main production years for male eels being between 10 and 15 and for females between 10 and 19 years old, respectively (Anonymous, 2010), the increase in the productivity of the lough would have affected the last of the 1941 glass eel cohort. This impact would continue with subsequent cohorts until the point in time when all arriving glass eels would benefit from the increase in the food supply. This is evident in Figure 5, which shows that silver eel output rose steadily for the 1943–1948 cohorts as more age groups profited from the increase in the food supply. In addition, this increase may also have contributed to a lower natural mortality rate for the 1944–1975 glass eel cohorts and as a consequence resulted in the high silver eel output from the mid-1950s to the early 1980s.

The decline that occurred for the early 1970 cohorts does not appear to be the result of a reduction in productivity as total phosphorous concentrations have remained high (Foy *et al*., 2003). This decline in cohort productivity coincides with the introduction of roach (*Rutilus rutilus*), which was first detected in the early 1970s (Cragg-Hine, 1973). Their abundance expanded rapidly, benefiting from the eutrophic conditions (Kennedy *et al*., 2001; Svardson, 1976; Tobin, 1990; Winfield *et al*., 1992, 1993), to become by far the most dominant species in terms of both number and biomass in the lough today. It is hypothesised that in Lough Neagh roach were outcompeting eel, possibly for both food and/or space, effectively reducing the lough's carrying capacity for eel. Roach have a diet similar to eel and Tobin (1990) found that the dominant prey item for roach in May was Chironomind larvae, which comprised over 60% of the diet by number. Copepods and *Gammarus* spp. were the next most important items numerically, both making up 10% of the food items. In August, prey items were similar to May, though the proportions varied, with chironomids comprising 40% of the diet at this time.

The evidence would therefore suggest that there have been two regime shifts within the lough that have impacted on eel, one positive, eutrophication, and the other negative, the introduction of roach. Previous studies have also found eel populations and output impacted by regime shifts (Dekker, 2004b; Poole *et al*., 2018). In the case of Lough Neagh and the Ijsselmeer the decline in the eel population commenced when recruitment was still high, the timing affected by local circumstances. The other study by Poole *et al*. (2018) describes a regime shift in the rivers Burrishoole (Ireland) and Imsa (Norway) where, in 1982 and 1988, the silver eel output dropped suddenly by 40% and 62%, respectively, stabilizing at this lower level. In both these cases the cause of the regime shift remains unexplained. This current study and those of Dekker (2004b) and Poole *et al*. (2018) demonstrate that an eel population can respond rapidly to environmental change. However, as a function of an eel's longevity and the fact that the population is rarely assessed during its first few years of continental life, the effect is seen some years after the initial impact of the ecological change that drove it.

Whilst the above may explain the situation in Lough Neagh post-1920 it does not explain the high level of total output and yield in the early part of the 20th century, 1905–1920. The level of output between 1911 and 1921 would appear high (Figure 3) assuming a pre-eutrophication carrying capacity of 1,000,000 kg or 26 kg ha^{-1} (Figure 5). This suggests a number of possibilities either individually or in combination: (a) that the model does not accurately reflect the dynamics of the population at that time and that the carrying capacity is greater than 20 kg ha^{-1}; (b) the level of exploitation in the silver eel fishery was higher than used in the model (12.2%); (c) the area of the lough was substantially larger than at present; (d) the size of the yellow eel catch had been overestimated, as suggested in Section 3.1; and (e) the lower size limit in the yellow eel fishery.

4.3 | Stock-recruitment relationship

The Beverton and Holt (1957) and Ricker (1954) stock-recruitment relationships are the two most commonly applied stock recruitment models (Hilborn & Walters, 1992). Both models were able to describe the relationship between the number of glass eels (stock) and the resultant output of silver eels (recruits) for the 1923–1997 cohorts (Figure 4). The Ricker model was not able to provide a valid solution for the two subsets of data: 1944–1975, and 1923–1943 and 1976–1994. It is evident that the data points (Figures 4 and 5) are not distributed at random and examination of the timeline indicates non-stationarity. This can be explained by a systematic shift from a period of high mortality for the 1923 to the early 1940s cohorts, then a decline, staying relatively stable before increasing for the post-1970 cohorts. It is suggested that the reason the Ricker model was able to provide a solution for the 1923–1997 data set is an artefact of the change in the stock dynamics such that the regulatory mechanism of the past does not apply to the current/more recent situation. This is considered to be a consequence of the change in the ecological state affecting the natural mortality rate.

The 1944–1975, 1923–1943 and 1976–1994 data sets would seem to indicate that the eel population in Lough Neagh is regulated by food availability. This could explain an asymptotic stock recruitment relationship as opposed to cannibalism or a density-dependent reduction in growth, coupled with size-dependent predation, resulting in a dome-shaped relationship (Ricker, 1975). This is because (a) cannibalism has not been reflected in diet studies (Anonymous, 1966; Frost, 1946; Marrion, 1986; Matthews *et al*., 2001) and (b) eel are predated upon by a number of predators: great cormorant (*Phalacrocorax carbo*), grey heron (*Ardea cinerea*), two species of sawbill ducks (*Mergus* spp), and mammals such as the Eurasian otter (*Lutra lutra*) and the mink (*Mustela* spp.). The numbers of these predators in Lough Neagh are not large enough to cause any significant impact over and above that which would be considered typical levels of natural mortality (Anonymous, 2010). In addition, neither fishermen nor the fishery managers have raised any concerns in relation to their natural predation on eels (Anonymous, 2010).

The model suggests an optimum stocking density of 300 glass eels ha^{-1} (11.5 M glass eels) and is comparable irrespective of the two ecological states (Figure 5). The optimum stocking density is similar to that reported by Moriarty (1999), Moriarty and Dekker (1997) and Rosell *et al*. (2005), but substantially lower than that stated by Bevacqua *et al*. (2019) of 10,000 glass eels ha^{-1} for the Camargue Lagoon. The lower optimum stocking density for Lough Neagh is not reflected in a lower silver eel output, the total silver eel output at the asymptote under the current ecological conditions being 26 kg ha^{-1} compared with 18 kg ha^{-1} for the Camargue (Bevacqua *et al*., 2019).

4.4 | Natural mortality

Estimates of annual natural mortality ranged from 0.017 to 0.142 year^{-1} (mean 0.073 ± 0.007 year^{-1}). These rates are comparable with those from Lake Hjälmaren, Sweden (Dekker, 2012) and from the rivers Imsa and Esva but are very much at the lower end of the range quoted (see Bevacqua *et al*., 2011; Supporting Information Table S2). The fact that an unknown proportion of glass eels bypass the traps at the Cutts will mean that these rates are minimum estimates. However, unpublished models (Aprahamian & Evans, in prep.) based on these mortality rates closely predict yellow and silver eel catch and silver eel escapement. This suggests that the proportion bypassing the traps is small in relation to the quantity trapped and transported to the lough.

Natural mortality was dependent on the initial stocking density of glass eels (Figure 6) and the perceived ecological status of the lough. Standardizing the natural mortality rate for the mean stocking density showed that mortality was fairly high at the start of the period (1920s cohort) to the early 1940s cohort and then started to decline. The lower mortality rate remained relatively stable until the early 1970s before increasing again (Figure 7). This suggests that the underlying mechanism is intracohort (*i.e*., competition for resources from eels within the same cohort) as opposed to intraspecific (*i.e*., predation from older eel cohorts) competition as suggested by Bevacqua (2009).

A similar density-dependent association between mortality and density has been reported elsewhere (Bevacqua *et al*., 2011; Lobón-Cerviá & Iglesias, 2008; Svedäng, 1999; Vøllestad & Jonsson, 1988). Bevacqua *et al*. (2011) also found that natural mortality increased with increasing mean annual water temperature. The higher levels of mortality cited in Bevacqua *et al*. (2011) at some locations in Sweden (Dekker, 2012), by McCarthy *et al*. (1994) and by Dekker (2000) of 0.1385 year^{-1} may reflect (a) a considerably higher glass eel settlement density and/or (b) that the estimate was based on a lower output than observed, as is perceived to be the case for the Swedish lakes (Dekker, 2012) and/or (c) the productivity of the waters is substantially lower than that of Lough Neagh.

4.5 | Implication for the decline and the recovery of the eel

Habitat loss has been implicated as one of the causative factors in the decline of the European eel, probably acting synergistically with others (Bevacqua *et al*., 2015; Dekker, 2004a; Feunteun, 2002; Moriarty & Dekker, 1997). The construction of water-retention structures, wetland reclamation, floodplain drainage and dredging have been considered to be the main causes of habitat loss. However, this study suggests there may be other more subtle, ecological impacts that affect the amount of habitat available to eel populations. In Lough Neagh eutrophication is considered to have increased the carrying capacity of its eel habitat by 50%. The prospect for increased output, however, remained unrealized following the introduction of roach and the subsequent decline in production by 35%. The eel is generally considered a dominant species in fresh waters, negatively impacting on others (Tesch, 2003). This may possibly be an oversimplification.

The major influence on the freshwater and estuarine environments that affect eel is those changes brought about through the Water Framework Directive (WFD), nevertheless the impact on eels remains a known unknown. It is anticipated that the outcomes of the WFD may be to the benefit of eels and in some circumstances, especially the reduction in pollutants, this will undoubtedly be the case (www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/ele.2737.nea.pdf). However, the findings from Lough Neagh suggest that a reduction in nutrients (nitrogen and phosphorous) leading to a change in trophic status will be to the detriment of the eel.

5 | CONCLUSION

The dynamics of the Lough Neagh eel population have changed over the last 100 years and are believed to be primarily driven by the ecological consequence of changes in water quality and the introduction and establishment of an invasive fish species. The carrying capacity increased from ≈1000 to 1550 t but has now fallen to ≈1000 t. This change in carrying capacity has only become apparent through analysis on a cohort basis extending back almost 100 years. The implications of the change in ecological state are less clear from the catch data alone. Lough Neagh is currently producing below capacity, and well below pristine capacity, as total input since 1988 has not been above 11.5 million glass eels (3833 kg), the number considered to be optimal (Figure 5). Eels can and do respond relatively quickly to changes in environmental circumstances, as can be seen by the rapid move between the two trophic states (Figure 5). Depending on the direction of change the analysis shows that natural mortality can fall by ≈30% or increase by 50% over a 10-year period.

This study has shown that the concept of a pristine level of silver eel output against which to manage the eel recovery, as set out in EC 1100/2007, may be unrealistic given the stock-wide ecological and environmental changes over the last 40 years. The EC Regulation sets a reference period of pre-1980 and as is evident this level of silver eel output from Lough Neagh is not likely to be achievable due to declining productivity (McElarney *et al*., 2021) and interspecific competition from an introduced species. The water quality objective of a reduction in nutrient concentrations (Northern Ireland Environment Agency, 2015) and the virtually impossible task of eradicating roach further reduces the likelihood of Lough Neagh being able to achieve pristine output, as defined in EC 1100/2007.

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CONFLICT OF INTERESTS

The authors declare no potential conflict of interests.

AUTHOR CONTRIBUTIONS

M.W.A. and D.W.E. conceived the study and should be considered joint first authors. D.W.E. collected and M.W.A. analysed the data, and both were equally involved in the interpretation of the data and the preparation of the manuscript. C.B. reconstructed the glass eel recruitment series, A.M.W. ran the SMEP II programme to estimate the migration probability of yellow eel age groups and Y.M. provided environmental data and MA statistical advice, and reconstruction of the flow regime. All authors approved the final version of the manuscript.

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