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Long-term variation in numbers and biomass of silver eels being produced in two European river systems

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The European eel (*Anguilla anguilla*) population has been in decline at least since the 1960s and reliable regional information, particularly on the spawner production and escapement (i.e. the silver eel life stage), is a requirement of the EU stock recovery regulation. Two comparable time series exist in Burrishoole (Ireland) and Imsa (Norway), with monitoring of total silver eel production since the early 1970s. Numbers of emigrating silver eels fell significantly ($p < 0.0001$) in the 1980s (breakpoints: Burrishoole 1982; Imsa 1988), in both catchments from >4000 eels per annum to ∼2000 eels per annum. The proportion of male eels dropped and the average size of female eels increased. Biomass of silver eels escaping has remained similar in Burrishoole (1.1/1.2 kg/ha), but not in Imsa (2.1/0.9 kg/ha) between the early period and the 2000s. Factors that govern the onset of eel maturation (silvering) and the annual production of silver eels are little understood. In this paper, the influence of time-lagged environmental variables on silver eel production is examined. Annual variation in the time series was partly (r^2 Burrishoole = 0.43, Imsa = 0.46) explained by variation in water temperature and water level. Annual number of migrating eels in both catchments was positively related to summer temperature and summer water flow, negatively related to summer temperatures in the previous year, and in the Burrishoole, also negatively related to high water levels in September/October. The models did not transfer well between catchments, indicating likely catchment specific environmental factors impacting on eel production. The reduction in eel numbers observed in both catchments, accompanied by the change in sex ratio and mean weight of females that contribute to maintain biomass production, calls into question the advisability of basing a spawner escapement recovery target on biomass alone, while numbers and proportions of males decline.

Keywords: *Anguilla anguilla*, annual production, biomass, silver European eel, temperature, water level

Introduction

European eel (*Anguilla anguilla*) spawn in the Sargasso Sea and recruit to the European and north African continental habitats following a *trans*-Atlantic larval migration. On arrival, the larvae metamorphose into glass eel and a proportion migrates upstream into inland waters where they are subject to many natural and anthropogenic pressures. The growth phase, when they are known as yellow eels, takes many years (sometimes decades) and varies between sexes, with males typically smaller and younger than females. The onset of sexual maturation or "silvering" occurs towards the end of their life cycle and is associated with preparation for the downstream and oceanic migration back to the Sargasso Sea (Tesch, 2003). Triggers for the silvering process, apart from size of the eel, are little understood, but are likely to be linked to growth (Durif *et al*., 2005). Little is known about the influence of environmental factors on this process. The long-term datasets in this article provide an opportunity to examine the role of time lagged environmental drivers, i.e. water temperature and level, on the amount of annual silver eel production.

The eel population, which is genetically panmictic (Palm *et al*., 2009), has been in decline at least since the 1960s, with a severe reduction in glass eel recruitment occurring in the early 1980s (Moriarty, 1990a; Dekker, 2003; Aalto *et al*., 2016; ICES, 2016). This prompted eel conservation and stock recovery measures within the European Union (European Council, 2007). EU Member States are now required by legislation (EC No. 1100/2007) to contribute to the restoration of the European eel stock by implementing eel management plans. The Regulation seeks to reduce anthropogenic mortalities to permit the escapement of 40% of the silver eel biomass relative to the best estimate of the escapement that would have existed if no anthropogenic influences had affected the stock (European Council, 2007). Setting the historical baselines and monitoring in biomass, rather than numbers, adds an extra challenge for Member States when assessing compliance with the Regulation, considering the overall paucity of relevant historical data and limited opportunities for ground truthing outputs from modelling exercises (e.g. Walker *et al*., 2011).

Long-term datasets of silver eel production and escapement are few, and many are based on fishery yield or some form of escapement estimate, using one or a combination of methods such as mark and recapture, acoustics and fisheries landings (Dekker, 2000a; Rosell *et al*., 2005; ICES, 2010). It is often difficult to determine the representativeness (proportion of run captured, bias in size or sex ratio) of such monitoring (Feunteun *et al*., 2000; Allen *et al*., 2006; MacNamara and McCarthy, 2014; McCarthy *et al*., 2014). Biases can occur when the fishing season does not cover the full migration period, when there is significant eel production downstream of the fishery area assessed, or when the implementation of management measures on fisheries introduces discontinuities in the data.

Direct assessments of silver eel leaving a given catchment are difficult to obtain due to the migration behaviour of the eel. Silver eels tend to migrate at night, during dark moon periods and in high water discharges making high capture efficiency difficult, especially in larger rivers (Vøllestad *et al*., 1986; Bruijs and Durif, 2009; Sandlund *et al*., 2017). Wolf traps (Wolf, 1951) or similar capture systems can be used to provide precise estimates of migrating eels and in some instances allow all silver eels to be counted and measured. Full quantification of the number, size and sex of silver eel leaving catchments has only been carried out on a few systems with trapping facilities (Vøllestad and Jonsson, 1986, 1988; Poole *et al*., 1990; Feunteun *et al*., 2000; Laffaille *et al*., 2006; Acou *et al*., 2009). Only the time series in the Imsa (Norway) and Burrishoole (Ireland) presented in this article include data collected before the collapse in recruitment during the 1980s. Such historical data are a requirement for setting historical baselines for the EU (Piggins, 1985; Vøllestad and Jonsson, 1986, 1988; Poole *et al*., 1990).

This study brings together the silver eel data sets from two contrasting watersheds in Ireland and Norway describing the stock composition and long-term trends of the silver eel production over a more than 40-year time span in rivers that have experienced little or no exploitation. Neither river has been stocked, nor had hydropower obstruction to migration. The eel data represent the complete annual number of escaping silver eels which are combined with environmental variables (temperature, water level) to explain how time lagged environmental drivers influence the year-to-year variation in annual numbers of migrating silver eel being produced in each catchment. Similarities and differences between the catchments are discussed, and the use of biomass as a management indicator in the light of continually falling numbers and changing sex ratios is questioned.

Material and methods

Site descriptions

The Burrishoole system in western Ireland (53° 56′ N, 9° 35′ W: Figure 1; and Supplementary Material) has a catchment area of 100 km^2 and drains through two channels, the Mill Race and the Salmon Leap, into the north-east Atlantic. The catchment has a total productive wetted area of 474 ha (449 ha lacustrine, 25 ha fluvial). Feeagh and Bunaveela, the two largest freshwater lakes, have mean depths >12 m, are oligotrophic (TP < 10 μg l^{-1}), coloured (c. 80 mg l^{-1} PtCo), and have low alkalinity (<20 mgl^{-1} $CaCO_3$) and pH (c. 6.7). Average combined water discharge at the river outlets is 4.2 m^3 s^{-1}, ranging between 0.4 and 13 m^3 s^{-1}, although higher discharges have been observed but not quantified. Strongly influenced by the Atlantic Ocean (Jennings *et al*., 2000), the climate is temperate and oceanic, with mild winters and cool summers. Maximum air temperature rarely exceeds 20°C, while minimum winter temperatures are usually between 2 and 4°C. The geology is predominantly of low buffering capacity, leading to acidic runoff, and overlaid with poorly drained predominantly peaty soils. There has been no commercial or recreational yellow or silver eel fishery and no stocking of eel.

The Imsa River in southwestern Norway (58° 54′ N, 5° 57′ E: Figure 1; and Supplementary Material) has a catchment area of 128 km^2. The catchment has a productive wetted area of 1160 ha (>800 ha of lake and ~360 ha fluvial habitat). Maximum depths of the five major lakes vary between 27 and 48 m. Water discharge at the river outlet varies between 0.5 and 30 m^3 s^{-1} (mean 4.5 m^3 s^{-1}). Similar to Burrishoole, climatic conditions are influenced by the Atlantic Ocean, and it is relatively warm, considering the northern location. Winter air temperatures are rarely below −4°C and summer temperatures rarely above 24°C. The Imsa has an average pH >6.8 and acid-neutralizing capacity ranging between 150 and 230 μeq l^{-1}. There has been no stocking of eel, but there was a restricted seasonal yellow and silver eel fishery upstream of the trapping station, which in the 1990s became relatively small due to fewer landowners participating in eel fishing and only hobby fishing, and the fishery closed from 2006. The catches, when known, from this limited fishery were taken into account in the production data in this study.

Silver eel trapping and recording of environmental variables

Trapping of downstream migrating silver eel has been in operation in Burrishoole since 1958 and in Imsa since 1975. The traps at the freshwater outflows of both catchments include Wolf type downstream traps of similar design (Wolf, 1951; McGrath, 1969) employing horizontal grids with 10 mm gaps on a 1:10 inclination. Trapping at Burrishoole involves a fish fence and wolf trap

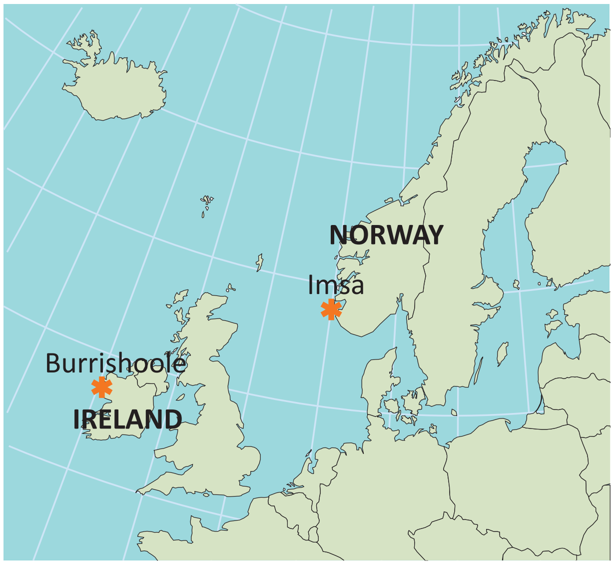

Figure 1. Map of northwestern Europe, showing the location of the two study sites (stars), Burrishoole in Ireland and Imsa in Norway.

on the Mill Race outflow installed in 1958 and a full flow controlled Wolf trap on the Salmon Leap outflow (McGrath, 1969 and map in the Supplementary Material) installed in 1970 (Poole *et al.*, 1990; Poole, 1994). Total annual captures probably represent about 90 ± 10% of the total run (Piggins, 1985). Years when extreme flood events led to known major losses of eel were 1978, 1984, and 1989 and these have been removed from the data.

In Imsa, trapping commenced in 1975 (Vøllestad and Jonsson, 1986, 1988). The total weight of the catch biomass from commercial silver eel fishing in the river upstream of Imsa was reported annually to the Research Station at Ims (Vøllestad and Jonsson, 1988). This was converted to numbers using the mean weight data of the eels caught in the trap that year, and added to the trap catch to give total silver eel production [in numbers and weight (kg) per ha]. No other fishing takes place on a regular basis (Vøllestad and Jonsson, 1988; Bergesen, pers obs.).

Daily water level and temperature (°C) were recorded on both the Burrishoole and Imsa outflow rivers. In Imsa, water discharge is estimated based on an empirical relationship between water level and discharge. The water level is recorded 15 m above the fish fence on the Mill Race and this is influenced by the amount of debris in the water. For this project, we used the lake water level, taken at the outflow of the lake 75 m upstream and away from any influence of the traps. Since the water level measurements from Burrishoole were obtained from two locations and with varying recorder setups and influences, a standardized Lake Feeagh water level time series was reconstructed, based on relationships estimated from periods with parallel recordings. Over the time-period, daily water temperature ranged from 1.5 to 23.5°C in Burrishoole and 0.2 to 24.2°C in the Imsa, with corresponding annual means of 9.2–12.4 and 7.7–10.7°C respectively. Imsa has warmer summer and colder winters than Burrishoole (Figure 2 upper graph). An examination of the temperature anomalies compared with the period 1971–2000 (1975–2000 for Imsa) indicated a period of warming in both catchments since 1997/1998 (Figure 2 lower graph).

Data collection and analysis

In both catchments, traps were attended at least once a day and all silver eels were counted and recorded. Annual numbers analysed in this paper are the summation of the daily trap counts from 1 May to the 30 April in the following year, called "Silver Season". Samples of descending silver eels were taken throughout the run, measuring total length (TL: to the nearest 0.1 cm Burrishoole, 0.5 cm Imsa) and weight to the nearest 1 g (Imsa) or 5 g (Burrishoole). Length and weight data were not collected in the Imsa between 1993 and 2011 and only batch weights were taken in Burrishoole between 1971 and 1975, 1978/1979 and 1980–1983. For consistency, the sex ratio was determined from length frequency analysis of the sampled eels. The overlap between the male and female modes was separated using the technique described by Bhattacharya (1967). These analyses were confirmed by random dissections (Burrishoole; $n = 1303$; 1986–2016; Imsa; see Vøllestad and Jonsson 1986) using gross macroscopic examination (Frost, 1945; Bertin, 1956).

Production of silver eel was calculated in numbers and biomass (kg) per hectare (wetted area) of the watershed upstream of the trap. Biomass was calculated using the mean weight and total count, including the reported catches upstream of the trap in the Imsa.

Structural changes, or breakpoints, in the time series were dated using the function breakpoint in the R package *strucchange* (R Core Team, 2016) where we assume that coefficients shift from one stable relation to another (e.g. Bai and Perron 2003). A Two Sample t-test was used to verify that the difference in the means of the two time series before and after the breakpoint was significant. After the structural breaks in the data were accounted for, time series analyses were performed (e.g. Wei, 2006) to evaluate possible serial dependencies. For each catchment, autoregressive (AR) integrated moving average models were fitted to each time series segment and tested whether the same AR structure existed within a catchment before and after the break. Finally, with the break points and potential time series structures established, generalized models (GLMs) with a Poisson error distribution were fitted to look for covariates that together with, or instead of, the AR terms explained the variance in the number of emigrating eels.

Statistical modelling of variation in eel run and the relationship to environmental parameters was carried out using the statistical software R (R Core Team, 2016). In the initial models of the annual eel count in both catchments, monthly averages for temperature [$T_{Y,\ M:}$ monthly mean water temperature from May the preceding year until November this year; the subscript Y denotes year, either the year of the eel counts (t) or the preceding year ($t\!-\!1$), while the subscript M denotes month (Jan–Dec)] and standardized water level ($WL_{Y,\ M:}$: monthly mean standardized water level from May the preceding year until November this year; the subscripts have the same interpretation as for water temperature) were used as explanatory variables. The water level time series was standardized, since we assumed that it is the variation around the mean that is informative and not the absolute value at some arbitrary location. The 2-year period was chosen, assuming that the various underlying processes preparing for migration may last for an extended period. Different river systems likely have different bottlenecks or optimal periods for maturation and migration, so we should initially include a long period in the analysis. The effects of temperature and water level were assumed

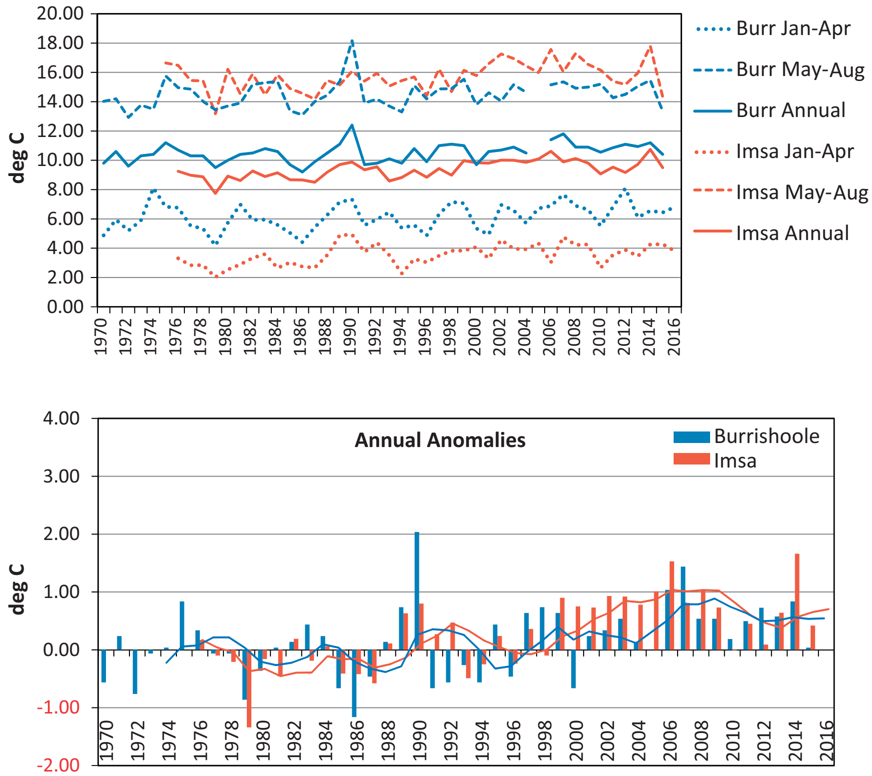

Figure 2. Mean winter, annual and summer water temperatures (upper graph), and water temperature anomalies with reference to the 1971–2000 period for the Burrishoole (Burr) and Imsa (1975–2000) (lower graph). In the lower graph, bars indicate annual water temperature anomalies and lines 5-year moving averages.

to be accumulated over a few months, but rather than determining these periods *a priori*, subsequent months that had the same effect on the model response were pooled to quantify the mean value over a longer period. For example, $T_{t-1,\ May\text{–}Nov}$ will denote the mean water temperature from May to November the preceding year.

A maximum linear regression model including all explanatory variables was simplified by stepwise reduction based on the Akaike information criterion (AIC) (Sakamoto *et al.*, 1986). If consecutive monthly averages for either water level or temperature had the same effect on the response, a model where these months were pooled together was also fitted and evaluated. A decrease in AIC of more than two was considered as sufficient support for retaining a variable in the model. Residuals were checked for normality and autocorrelation, since the migrating part of a population in subsequent years may be correlated, especially for species with a wide age distribution such as eel.

Results

Annual variation in number of silver eels

There was considerable annual variation in silver eel counts in both Burrishoole and Imsa rivers (Figure 3). In both rivers, there was a downward shift in the 1980s in the annual numbers of migrating eels. In Burrishoole, breakpoint analysis indicated a break in the time series after 1982 (95% CI = 1980–1985), when the average count changed significantly (two sample t-test; $p < 0.0001$) from 4719 eels to 2821 eels. In Imsa, breakpoint analysis indicated a break after 1988 (95% CI = 1987–1990) when the average count changed significantly (two sample t-test; $p < 0.0001$) from 5815 eels to 2201 eels (data supplied in the Supplementary Tables S1 and S2). It should be noted that before the abrupt shifts, the average number of eels in Imsa was higher than in Burrishoole, while after the shift, the counts were higher in Burrishoole (Figure 3).

For Burrishoole, after the break in 1982 had been accounted for, no significant AR terms were found in either of the time series segments. For the Imsa time series with a break in 1988, the AR model with lag 1 year was close to being significant before the break [AR(1) = −0.404; $p = 0.085$], and not significantly different from the model fitted to the time series after the break. Assuming the same AR structure before and after the break, the AR model still showed a weak significance [AR(1) = −0.281; $p = 0.061$]. A negative AR(1) coefficient indicates a temporal pattern where high emigration in 1 year may lead to a reduced emigration the next year.

Influence of water temperature and level on annual eel run

Finally, with break points accounted for and weak serial dependencies established for the time series, we fitted GLMs with a Poisson error distribution to the annual eel runs. The 1 year lagged autocorrelations of the time series were better explained by lagged covariates of water temperature, so no AR terms were retained in the models.

By fitting a model to the whole detrended time series, i.e. breaks accounted for, we assume that the modelled relationships were the same in both periods and that the covariates cannot explain the shift in mean level. Models fitted to the two periods separately gave similar results, and there was no obvious relationship between the shift in eel numbers and the temperature or water level variables, which supported these assumptions. The fit of the models (Table 1) shows that the eel run in most years is well described by the model (Figure 4), although a few years have large residuals, indicating that there are some environmental variables affecting the eel run in some years that are not accounted for by the model. The years with large residuals occur in different years in the two systems (Figure 4).

The maximum model for Burrishoole, including all explanatory variables, had an AIC of 683.5. Stepwise removal of variables that did not improve the AIC, and biologically sensible pooling of months that had the same effect on the response, resulted in a simplified model with four variables and an AIC of 670.6 and $R^2 = 0.43$ (Table 1).

The detrended eel numbers in Burrishoole can be explained by a negative relationship with a warm previous season ($T_{t-1,\ May\text{–}Nov}$ - mean water temperature over all months from May to November), and a positive relationship to the current year's conditions in August (both temperature and water level), while high mean water levels in September and October caused a decrease in the number of migrating eels (Table 1).

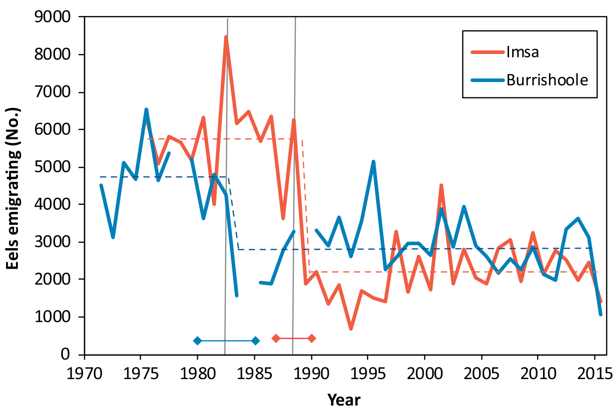

Figure 3. Annual counts of eels emigrating from the Burrishoole and Imsa Rivers between the early 1970s and 2015, with means for each period indicated by dashed lines. The breakpoints are indicated by vertical dotted grey lines and the 95% *CI*s around the breakpoints are shown above the x-axis.

The maximum model for Imsa, including all explanatory variables, had an AIC = 652.6. Applying the same variable selection approach as for Burrishoole resulted in a model with an AIC = 644.8 and $R^2 = 0.48$ (Table 1). The detrended eel numbers in Imsa have a negative relationship with the mean temperature in June and July the previous year, and a positive relationship with mean temperatures in September and October the previous year. There was a positive relationship with mean temperatures in the summer (June and July) of the same calendar year, and with the mean standardized water level in January and February in the same year (Table 1).

When Imsa data were used to validate the Burrishoole model, the validation R^2 was close to zero. A similar result was obtained using Burrishoole data to validate the Imsa model, i.e. R^2 almost equal to zero. Thus, predicting the quantity of annual eel runs in one of the catchments from a model fitted in the other catchment gave poor results.

Size and sex

We used length as the indicator of eel size, while noting that there is a highly significant exponential relationship between length and weight allowing conversion to biomass. Although the Burrishoole eels were on average 10% heavier than the Imsa eels of the same length, the slopes in the log-log models were similar [Burrishoole log(Weight) = 3.11*log(Length)–6.72, $R^2 = 0.94$; Imsa log(Weight) = 3.12*log(Length)–6.83, $R^2 = 0.97$].

Table 1. Significant variables and their coefficients and significance levels for the Burrishoole and Imsa run models.

	ΔAIC	R^2	Variable	Estimate	s.e.	t value	*p*
Burrishoole	−13.0	0.43	(Intercept)	−3083	2377	−1.30	0.200
			$T_{t-1,\ May\text{–}Nov}$	−345	127	−2.70	0.010
			$T_{t,\ Aug}$	486	114	4.26	0.0001
			$WL_{t,\ Aug}$	685	263	2.60	0.013
			$WL_{t,\ Sep\text{–}Oct}$	−546	239	−2.28	0.028
Imsa	−7.8	0.48	(Intercept)	−5862	2510	−2.34	0.025
			$T_{t-1,\ Jun\text{–}Jul}$	−290	113	−2.56	0.015
			$T_{t-1,\ Sep\text{–}Oct}$	499	177	2.82	0.008
			$T_{t,\ Jun\text{–}Jul}$	291	107	2.72	0.010
			$WL_{t,\ Jan\text{–}Feb}$	−384	176	−2.18	0.036

T, water temperature (°C), *WL*, water level (m in Imsa, standardized lake water level in Burrishoole), *t*, year, and *t*−1, preceding year.

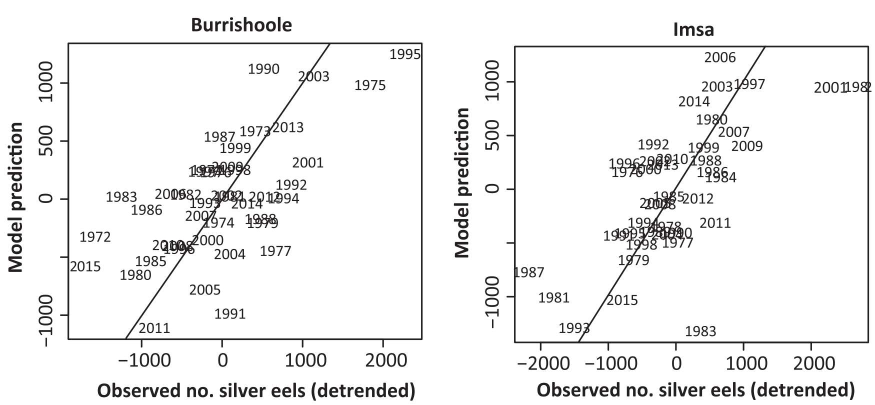

Figure 4. Model run predicted outputs plotted against detrended silver eel counts for the Burrishoole and Imsa catchments. The straight line gives the 1–1 relationship.

There was a strong sex-related bimodal distribution of eel length in both Burrishoole and Imsa although the proportions differed between locations and over time (see Figure 5 for sample years). In Burrishoole, male eels ranged from 27.6- to 45.4-cm body length (dissected eels, $n = 445$) and females ranged from 37.5 to 105.3 cm (dissected eels, $n = 859$). Only three females were <40 cm. In Imsa, male eels ranged from 32.5- to 46.0-cm body length ($n = 119$) and females from 39.0 to 107.0 cm ($n = 4164$).

A multivariate linear regression model showed differences in the size of eels for each sex; both over time and between locations (see Supplementary Table S2). For male eels, and noting the large disparity in numbers of males between the two catchments, the males in Burrishoole were significantly smaller than those in the Imsa (−3.7 cm; $p < 0.0001$) in all periods. The males in Burrishoole decreased significantly in size by decade ($p < 0.001$) over the sample period, with males averaging 37.0 cm in the 1980s, 36.7 cm in the 1990s and 35.7 cm after 2000 (Figure 6). There were too few males in the Imsa to examine any change over time.

The female length model was highly significant ($p < 0.001$) with both decadal differences in each catchment and a significant interaction between catchments, noting the missing data in the Imsa in the 1990s and 2000s, and with competing tendencies in the 2010s when the Burrishoole females decreased in length while Imsa females increased. The female eels in Burrishoole were significantly shorter (−11.6 cm; $p < 0.001$) than those in the Imsa in all years sampled (Figure 5; and Supplementary Material). The female eels in Burrishoole increased in length from the 1970s until 1998, stabilised until 2005 and then started to decline in size again (Figure 7), averaging 50.3 cm in the 1970s/1980s, 52.0 cm in the 1990s, 52.8 cm in the 2000s and 49.6 cm in the 2010s (Figure 7; and Supplementary Table S3). In the Imsa, females were similar in length from 1982 to 1991 (61.9 cm in the 1980s and 62.8 cm in 1991/1992) and then increased to 68.7 cm in the last 4 years of the 2010s (Figure 7).

There has been a drop in the proportion of male eels in both catchments, in Burrishoole from >55% male before 1985 to

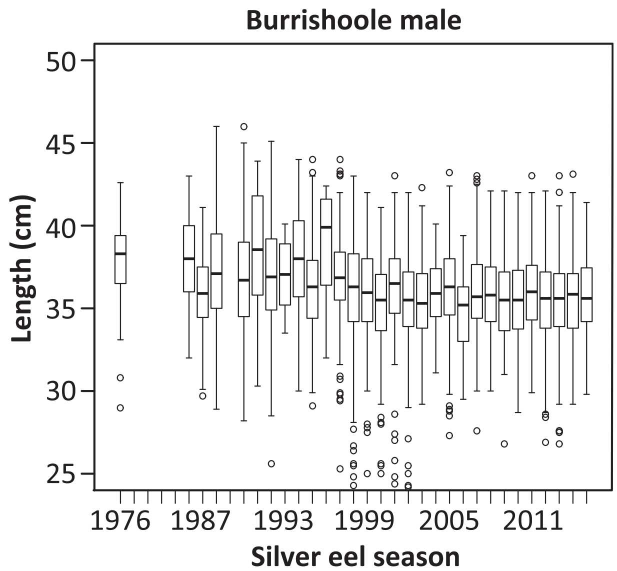

Figure 6. Boxplots for length (cm) of male silver eels in Burrishoole. The central box depicting the middle half of the data (25th–75th percentiles), the horizontal line across the box marks the median, the whiskers indicate the main extent of the connected data (~1.5*interquartile range (IQR)) and extreme values are indicated by starbursts.

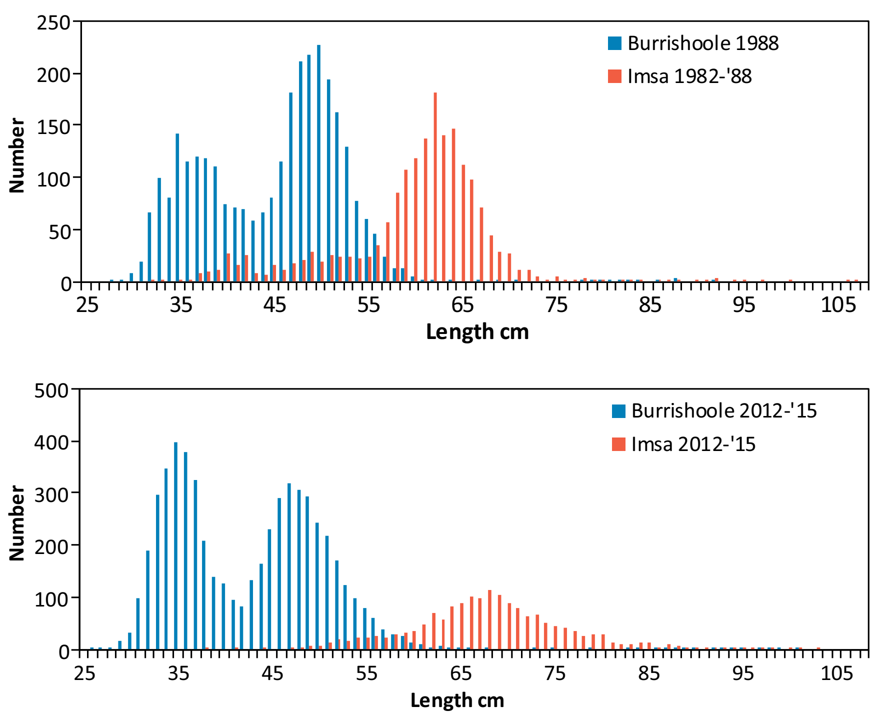

Figure 5. Length frequency distributions for Burrishoole 1988 ($n = 3003$) and Imsa 1982–1988 ($n = 1830$) (upper graph) and for 2012–2015 Burrishoole ($n = 5665$) and Imsa ($n = 1720$) (lower graph).

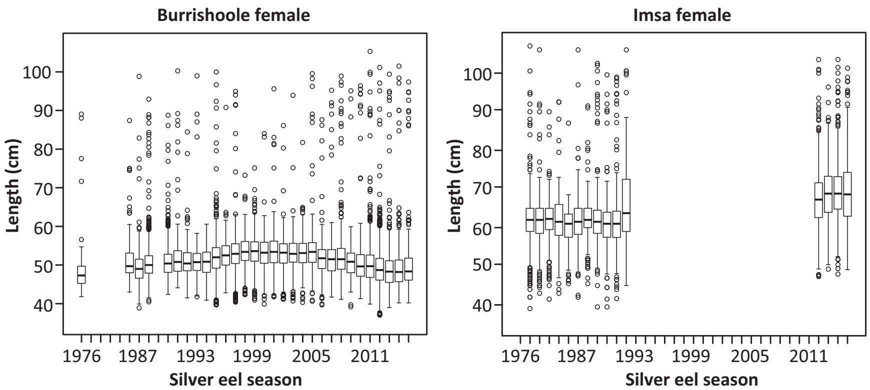

Figure 7. Boxplots for length (cm) of female silver eels in Burrishoole and Imsa. The central box depicting the middle half of the data (25th–75th percentiles), the horizontal line across the box marks the median, the whiskers indicate the main extent of the connected data (~1.5*IQR) and extreme values are indicated by starbursts.

about 35% in the last decade, and in the Imsa from 5.6% in the early 1980s to <0.2% in the last 5 years (Table 2).

Production

The average silver eel production in numbers per ha was higher in Burrishoole than in Imsa for both periods (Analysis of variance (ANOVA), $p < 0.0001$) (pre- and post-1982 in Burrishoole; pre- and post-1988 in Imsa), but the Imsa had a significantly (ANOVA, $p < 0.0001$) higher production in biomass per ha due to the larger size of the female eels (Table 2, Figure 8). In Burrishoole, the reduction in numbers over time was accompanied by a slight, but not significant ($p = 0.134$) increase in biomass while, in contrast, both the numbers and biomass fell significantly (ANOVA, $p < 0.0001$) in the Imsa (Figure 8; ANOVA outputs supplied in the Supplementary Table S4). This was due to the larger reduction in the number of males in the Burrishoole and the increase in the average weight of the females while the number of females remained similar in both periods (Table 2). In the Imsa, males were relatively few in both periods. The reduction in numbers of females outweighed their increased average size, leading to the reduction in both numbers and biomass in the Imsa.

Discussion

The Burrishoole (Ireland) and Imsa (Norway) rivers have been independently monitored using full river trapping systems of similar design (see McGrath, 1969) for >45 years. Although the eel stock in each catchment has its own particular characteristics, some of the similarities are striking. In the 1980s, both catchments experienced a sudden drop in numbers of eels emigrating, a reduction in the proportion of males in the silver eel run and an increase in the size of females. It seems likely that maturation (silvering), and hence the level of annual production of silver eel, was positively related to summer temperature and summer water flow, negatively related to summer temperatures in the previous year, and in the Burrishoole, also negatively related to high water levels in September/October.

Both catchments have experienced higher temperatures in the last 20 years compared with the 30 years before that, the Imsa more so than Burrishoole (Fealy *et al.*, 2014; this paper). Burrishoole has also shifted towards mesotrophic conditions since the 1950s, associated with the commencement of commercial coniferous plantations (Dalton *et al.*, 2014). Untangling the relative influence of different factors, such as temperature, eel density and trophic changes, on eel stocks is difficult. Changing eel growth across Europe has been associated with rising temperature over the last century (Daverat *et al.*, 2012) and the silver eel run has been commencing earlier (on average 0.8 days/year) in Burrishoole (Sandlund *et al.*, 2017). However, to our knowledge there are no previous studies showing how the level of annual production of silver eel might be influenced by time-lagged environmental factors.

Little is known about the mechanism that governs the decision to mature and migrate, once an eel is in the optimum size range for the river, or about the factors that influence the physiological readiness to migrate, although these are likely to involve significant changes in body constitution and energy (e.g. fat, protein, and dry matter) and also raised cortisol levels in the autumn linked to energy mobilisation (Van Ginneken *et al.*, 2007). The environmental or physiological conditions that trigger the onset of maturation and silvering are still poorly understood (Durif *et al.*, 2009).

Environmental variables (e.g. water level, water temperature) likely to influence the onset of silvering, using variables from the year of the migration and from the preceding year, explained approximately half the variation in annual eel count in each catchment. Although there was little evidence of a regular pattern of low years following high years in either catchment, high summer temperatures were associated with greater numbers migrating in that year, and consequently lower numbers migrating the following year. This was shown by a significant relationship with temperature in June/July (Imsa) and May/November (Burrishoole) in the previous year, and high temperatures in the current year in June/July (Imsa) and in August (Burrishoole). Water level in August in Burrishoole was also positively related to eel count. The onset of migration in the Loire River (France) was correlated with August temperature, discharge and sunshine hours (Durif and Elie, 2008). Temperature-related increases in growth and physiological activity could encourage a higher proportion of eels to reach the required physiological threshold switch for the onset of silvering in that year. Consequently, in the following year, there will be a lower proportion of eels near that threshold as they had migrated in the previous season and therefore less eels are available to migrate in those years following high temperatures. The significant positive relationship in Imsa, with high

Table 2. Five-year mean total biomass (kg), % males and production in weight and number per hectare of the total run of silver eels, and separately for males and females in the Burrishoole and Imsa Rivers.

Year	Count	Total B iomass kg	Total Output kg/ha	Total Output Nos/ha	% Males	Biomass Males kg/ha	Biomass Females kg/ha	Number Males Nos/ha	Number Females Nos/ha
Burrishoole									
1970–1974	4360 (857)	362 (67)	0.8	9.2					
1975–1979	4639 (804)	561 (126)	1.2	11.5	60.4	0.4*	0.5*	6.29*	4.09*
1980–1984	3061 (1419)	540 (129)	1.1	7.5	55.0				
1985–1989	2464 (683)	492 (141)	1.0	5.2	38.2	0.20	0.91	2.07	3.51
1990–1994	3217 (453)	683 (83)	1.4	6.8	33.4	0.23	1.21	2.34	4.45
1995–1999	3190 (1128)	720 (229)	1.5	6.7	27.7	0.17	1.35	1.93	4.80
2000–2004	3248 (618)	681 (146)	1.4	6.9	35.3	0.20	1.24	2.43	4.44
2005–2009	2492 (284)	549 (63)	1.2	5.3	29.9	0.13	1.03	1.62	3.70
2010–2014	2842 (742)	500 (110)	1.1	6.0	39.7	0.19	0.86	2.42	3.58
2015	1073 (–)	206 (–)	0.4	2.3	44.7	0.08	0.36	1.01	1.25
Imsa									
1975–1979	5611 (500)	2316 (180)	2.0	4.8					
1980–1984	6288 (1583)	2627 (639)	2.3	5.4	5.6	0.038	2.437	0.344	5.721
1985–1989	4760 (1947)	1994 (800)	1.7	4.1	2.7	0.012	1.707	0.107	3.996
1990–1994	1560 (574)	892 (270)	0.8	1.6	3.9	0.007	0.762	0.058	1.494
1995–1999	2099 (808)								
2000–2004	2600 (1144)								
2005–2009	2595 (632)								
2010–2014	2377 (311)	1434 (201)	1.2	2.0	0.1	0.001	1.236	0.003	2.002
2015	1398 (–)	879 (–)	0.8	1.2	0.2	0.000	0.760	0.003	1.202

*SD*s are in brackets. Blanks signify absent data and * is for 1976 only.

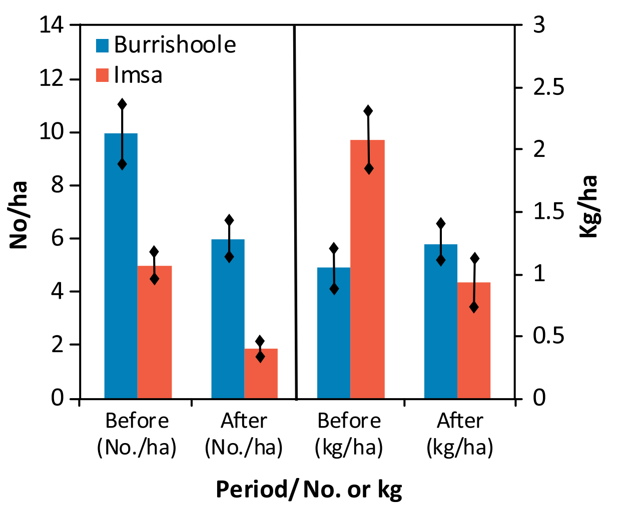

Figure 8. Production in numbers (left panel) and biomass (right panel) per hectare for the Burrishoole and Imsa catchments, averaged for the periods before and after their respective change in the 1980s (1982 Burrishoole; 1988 Imsa). The black vertical lines indicate the 95% *CI*s.

temperatures in September/October leading to a higher migration in the following year, also supports that argument, where eels that were not quite at the threshold in the current season may have a longer growing season thereby facilitating silvering in the following year.

The relationship with water level in the Imsa in January and February may be related to an interaction between warm winters and higher precipitation or less ice, and therefore earlier influences on eel physiology than in colder drier winters. Such cold winters usually do not occur in Burrishoole. In Burrishoole, eel counts were lower than expected with increasing water level in September/October. This is counter-intuitive, unless we consider that this was an artefact related to high floods reducing trapping efficiency, which is considered unlikely.

The size of female silver eel and proportion of males observed in the two catchments in this study are consistent with the cline in these parameters demonstrated for American eel *Anguilla rostrata* (Helfman, 1988; Oliveira, 1999; Jessop, 2010) and European eel (Vøllestad, 1992), with less males and larger females with increasing latitude and distance from the Sargasso Sea. In the 1960s, partial trapping in Burrishoole indicated a silver eel male sex ratio of over 94% (Piggins, 1985), a fact supported by a yellow eel fyke net survey (Moriarty, 1974). The male ratio declined to circa 30% in the 1980s (Poole *et al.*, 1990), and is currently around 44% in the most recent decade (this study). In contrast, the silver eel run in Imsa was dominated by females in the 1970s and 1980s, with the male sex ratio between 1 and 7% (Vøllestad and Jonsson, 1986, 1988), and this has now decreased to <0.5% males. These changes in sex ratio in both catchments have been accompanied by an increase in the average size of females. The number of females per annum in Burrishoole has remained similar while it has fallen in the Imsa since the mid-1980s. Andersson *et al.* (2012) noted a considerable decline in escapement of eels in the southern areas of Sweden over the past 50 years, but particularly in the 1960s and 1970s, inferred from fishing records and fisheries independent surveys. It seems likely that falling density of eel leads to lower proportions of males and some compensation by an increase in mean weight of silver eel (De Leo and Gato, 1996; Andersson *et al.*, 2012; this study). The ratios of number to biomass observed in this study are probably catchment specific and are likely to vary with latitude (Vøllestad, 1992) depending on the proportion and size of the female eels present in the catchments.

Production and escapement estimates are rare, especially before the 1980s (see review Supplementary Table S4) with the majority based on fishing yield or on estimates of escapement using mark-recapture or partial counts. In recent years, the Burrishoole has been producing about 1.1–1.4 kg/ha or 5.3–6.9 eels/ha, which is a similar weight per hectare as estimated for the Fremur catchment (1.3 kg/ha; Feunteun *et al*., 2000), the Shannon (1.5–1.6 kg/ha; MacNamara and McCarthy, 2014) and the Erne (1.5–1.7 kg/ha, McCarthy *et al*., 2014). However, it is a lower production in weight per hectare than estimated for the Imsa (3.51 kg/ha; Vøllestad and Jonsson, 1988), the Oir (4.8–6.9 kg/ha; Acou *et al*., 2009) and the Lake Ijsslemeer (4.4 kg/ha; Dekker, 2000b). Production in the Burrishoole and these other freshwater catchments is much lower than estimated for coastal lagoons in south-western France (Bages-Sigean: 30 kg/ha; Amilhat *et al*. (2008) and the Mediterranean (Comacchio: 20 kg/ha; Rossi, 1979, Sardinia: 19 kg/ha; Rossi and Cannas, 1984). High yields have also been reported from some freshwater catchments where the yield was maintained by active transport and stocking of glass eels and elvers, such as Lough Neagh in Northern Ireland (>20 kg/ha; Moriarty, 1988).

Although the biomass production in Burrishoole has remained similar since the 1970s, the number of eels has decreased from an average of 11.5 eels/ha in the late 1970s to an average of 5.8 eels/ha in the 2000s. Production in 2015 was the lowest on record in the Burrishoole and second lowest in Imsa. In contrast, both biomass and numbers have fallen in the Imsa over a similar period. A decline in silver eel production has also been reported in the Irish River Shannon, at least since 1992, but due to changing fishery management practices it is difficult to understand the dynamics of that stock (Moriarty, 1990b; McCarthy and Cullen, 2000; MacNamara and McCarthy, 2014).

Mature eels are sexually dimorphic in size, with males being smaller than females. Both genetic and environmental factors have been implicated in sex determination and, for European eel, it has been related to various factors including population density, levels of recruitment and catchment characteristics (Davey and Jellyman, 2005). In general, male silver eels are more abundant at high densities whereas females predominate at lower densities (Parsons *et al*., 1977; Vøllestad and Jonsson, 1988). It is generally understood that in the European eel, optimum size for each sex is promoted, rather than age, and that this optimum size, especially in females, varies with distance from the Sargasso and with latitude (Vøllestad, 1992). The majority of female silvers in Imsa are larger than in Burrishoole (this article; Haraldstad *et al*., 1985; Vøllestad and Jonsson, 1986; Poole *et al*., 1990; Poole and Reynolds, 1996), and in recent years this difference has increased.

Sex ratios can vary widely between catchments and over time (Parsons *et al*., 1977; Jessop, 1987; Poole *et al*., 1990; Oliveira, 1999; Oliveira and McCleave, 2000; Oliveira *et al*., 2001; Tesch, 2003). Changes in stocking densities (Parsons *et al*., 1977; Wickström *et al*., 1996) and natural recruitment (Rossi *et al*., 1988; Bark *et al*., 2007) have been implicated in altered sex ratios in some systems. It seems likely, therefore, that the changes observed in the Burrishoole and Imsa Rivers are a response to the observed low recruitment, which has been consistent with the decline observed across Europe since the early 1980s (Poole, 1994; Bornarel *et al*., 2017; Durif *et al*., in prep.), with falling local stock densities and maybe also changes induced by rising temperatures and catchment enrichment. Bark *et al*. (2007) illustrated temporal changes in population density and population structure in the River Piddle and other rivers in England and Wales, where a decline in population density since the mid-1970s was accompanied by a profound change in population structure, from one dominated by small eels to one currently dominated by large eels, clearly suggestive of a major recruitment failure. In rivers where eel populations were stable, the populations were male biased, while rivers with declining populations were female biased (Bark *et al*., 2007). Similarly, Laffaille *et al*. (2006) associated a shift from male to female dominance with a falling number of silver eels in the Fremur in France in an 8-year period after 2000, likely due to a number of factors including the installation of eel passes on the main hydraulic engineering structures in 1992 and 1996.

Although sex ratio and eel size have been changing over a longer time scale in Burrishoole (Poole *et al*., 1990), likely influenced by environmental changes in the catchment (Dalton *et al*., 2014), it is not easy to find an explanation for the sudden drop in numbers of eels in Burrishoole and in Imsa, particularly as the annual silver eel run is composed of up to 20 or more age classes of eel (Poole and Reynolds, 1996; Durif *et al*., in prep.). The 6-year difference between catchments in the main drop in numbers during the 1980s is also difficult to explain.

The collapse in recruitment observed in the 1980s across Europe was preceded by a longer-term decline in landings, indicating a probable decline in the continental potential spawning stock (Dekker, 2003) and leading to a conclusion that insufficient spawning stock biomass might have caused the recruitment collapse. More current observations indicate possible Allee-effects (Allee, 1931), or depensatory mechanisms (Hilborn and Walters, 1992), taking place in the stock–recruitment relationship and likely caused by a disruption in the social mating system below a minimum spawning density (Dekker, 2004, 2008). The spawning target set in the EU Regulation is based on biomass of the combined sexes (European Council, 2007). If the demographics (e.g. numbers, size, and sex ratio) of the eel stock are changing, as indicated in these catchments (this article), and other areas (e.g. De Leo and Gato, 1996; Bark *et al*., 2007; Andersson *et al*., 2012), it is possible that by concentrating on a biomass only approach we may overlook social aspects of eel reproduction and miss the opportunity to positively influence the spawning stock recovery and further contribute to the decline in the stock.

In conclusion, annual counts and biomass of silver eels in the Burrishoole and Imsa rivers were remarkably similar: the numbers of eels emigrating from the 1980s to present decreased in both catchments, the Imsa lagging 6 years behind the Burrishoole. In both catchments, the proportion of silver males decreased and the size of the females increased, likely due to a combination of stock density and changing productivity of the catchments. Silver eel runs were more important after warm summers and this resulted in a reduction of the number of silver eels in the following year. Warm autumn temperatures in the Imsa may extend the growing season, facilitating more eels to silver the following year. The reduction in numbers observed in both catchments, accompanied by the change in sex ratio and mean weight of females that contribute to maintain biomass production, especially in the Burrishoole, calls into question the advisability of basing the silver eel recovery target under the EU Regulation solely on biomass, while numbers and proportions of males continue to decline.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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