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Silver eel (*Anguilla anguilla*) population dynamics and production in the River Shannon, Ireland

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Abstract – The European eel (*Anguilla anguilla*) is in decline throughout its distribution and accurate regional information, particularly on the silver eel life-stage, is an essential component of stock recovery plans. Therefore, silver eel population dynamics and production were investigated on the Irish River Shannon. Size frequency analysis during the annual seaward migration showed that between 2008 and 2011, seasonal trends in both sex ratio and female size occurred. Catch analysis and mark-recapture experiments were undertaken during the same period to determine silver eel production. Due to extreme discharge in 2009, no catch data was available for 17 nights, and a novel protocol was developed using a Dual Frequency Identification Sonar (DIDSON) to quantify silver eel migration. In 2008, silver eel production was estimated at 57.3 t (1.35 kg·ha^{-1}), but an additional 18.3 t of potential migrants were estimated to have been removed by the summer yellow eel fishery. In 2009, following closure of the yellow eel fishery, silver eel production increased to 68.6 t (1.62 kg·ha^{-1}), before declining to 62.7 t (1.47 kg·ha^{-1}) in 2010 and 61.6 t (1.45 kg·ha^{-1}) in 2011. Modelling, based on long-term stocking data (1959–2011) and retrospectively estimated silver eel production (1992–2007) suggests that despite commercial fishery closure on the river, the decline in River Shannon silver eel production will continue for at least the coming decade.

Key words: *Anguilla*; downstream migration; DIDSON; population model; seasonality; silver eel production

Introduction

European eel (*Anguilla anguilla*) spawn in the Sargasso Sea and recruit to continental habitats after a trans-Atlantic migration. Growth takes place in freshwater and coastal areas for up to 20 or more years (yellow eel life-stage). A metamorphosis to the silver eel (spawner) life-stage then occurs, followed by a return migration to the Sargasso Sea (Tesch 2003). Throughout Europe, *A. anguilla* recruitment is declining, and regional studies have indicated that the continental stock (yellow and silver eels) is also in decline (e.g., Moriarty & Dekker 1997; Andersson et al. 2012). Appropriate management of eel stocks has been the subject of much discussion (Moriarty & Dekker 1997; Feunteun 2002; Russell & Potter 2003), but the protection of silver eels leaving continental habitats is now considered fundamental to boosting recruitment levels (ICES 2006). Consequently, the European Union (E.U.) stock recovery plan (EC No. 1100/2007) specified a target of 40% silver eel biomass escapement, measured with respect to undisturbed conditions, to be achieved by each Member State.

As silver eels are deemed to be the critical component of *A. anguilla* stock recovery, it is essential to understand all aspects of this life-stage. However, due to the extensive oceanic migration, this is complex and expensive. Despite some recent advances in our understanding of silver eel biology in the open ocean (Tsukamoto 2009; Righton et al. 2012), widespread monitoring is still somewhat limited pending further technological developments. Therefore, conservation efforts must primarily focus on silver eels in freshwater and coastal areas (e.g., Robinet et al. 2007). In response to the E.U. stock recovery plan, Eel Management Plans (EMPs) were developed by

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each Member State for their river basin districts, which outline specific actions necessary to achieve the overall 40% silver eel biomass escapement. Due to the lack of basic quantitative silver eel data on many European rivers, modelling rather than field data formed the basis of many of these strategies (e.g., Aprahamian et al. 2007; Robinet et al. 2007). However, accurate empirical information on silver eel populations is essential to develop management actions and verify the modelling approach adopted in the EMPs and elsewhere. Some field studies, ranging from minimally impacted habitats (Davidsen et al. 2011) to fishery/hydropower-impacted rivers (Klein Breteler et al. 2007; Winter et al. 2007), have provided useful data on silver eel migration. However, a series of intensively monitored, representative 'index' sites are necessary to identify population trends and to quantify specific regional contributions to the panmictic spawning stock (e.g., Amilhat et al. 2008; Bilotta et al. 2011; Charrier et al. 2012). This Europe-wide approach will ensure appropriate decisions concerning eel management are made collectively, at both regional (river basin) and international (E.U.) level.

One such index site is the Irish River Shannon. The eel populations of this river, which is regulated for hydropower generation, are well researched (e.g., McCarthy & Cullen 2000; McCarthy et al. 2008; Yokouchi et al. 2009; MacNamara & McCarthy 2012) and long-term, reliable eel fishery records are available. A commercial eel fishery formerly operated on the river, but in recent years, only conservation ('trap and transport') silver eel fishing is permitted. In this study, silver eel population dynamics and production were investigated during a 4-year (2008–2011) monitoring programme. Mark-recapture experiments and catch analysis were undertaken during the commercial (2008) and conservation (2009–2011) fishery, enabling the impact of yellow eel removal on silver eel production to be quantified. The use of an alternative monitoring technique (i.e., multibeam sonar) during a temporary period when catch records were not available was also evaluated. Retrospective (1992–2007) silver eel production was estimated, and a time-lagged input–output model was developed using long-term (1959–2011) juvenile stocking records to predict future silver eel production. The results are discussed in relation to other available Irish and European data, and the implications for stock recovery.

Materials and methods

Study area

The Shannon International River Basin District drains an area of 18 000 km^2 into the North Atlantic, and includes Ireland's longest river, the River Shannon (359 km of main channel), which lies predominantly in the central lowlands. The river (186 m^3·s^{-1} mean annual discharge) has been regulated for hydropower generation since the 1920's, following construction of an 86 megawatt hydropower station (Ardnacrusha) and regulating weir (Parteen) near the tidal limit (Fig. 1). The cascade catchment (defined here as the area of the catchment upstream of the lowermost hydropower dam, i.e., Ardnacrusha) is 10 400 km^2. The total wetted area of the cascade catchment, expressed in ha to facilitate comparison with other eel production estimates (i.e., in kg·ha^{-1}), includes 38 771 ha of lake habitat and 3695 ha of fluvial habitat (DCENR 2008). The three main lakes of the catchment are Lough Derg (11 635 ha), Lough Ree (10 500 ha) and Lough Allen (3500 ha) (Fig. 1), but six other lakes are >900 ha, and can be generally characterised as shallow and mesotrophic to eutrophic (McCarthy et al. 2008). Daily water temperature, recorded at Parteen regulating weir, varies from 1.0 to 24.0 °C (11.7 °C mean annual water temperature).

Commercial eel fishing took place throughout the catchment (Quigley & O'Brien 1996; McCarthy & Cullen 2000; McCarthy et al. 2008) until closure was specified as a requirement of Ireland's EMP (DCENR 2008). The yellow eel fishery, which involved longline and fyke net capture during the summer months (see details in McCarthy et al. 2008; Yokouchi et al. 2009), ceased in 2009. The commercial silver eel fishery, which consisted of stow net capture at river and lake outlet sites in autumn/winter (see details in McCarthy & Cullen 2000; McCarthy et al. 2008) ceased prior to this, in 2008. As a hydropower mitigation measure specified by Ireland's EMP (DCENR 2008), a catchment-wide conservation ('trap and transport') silver eel fishery was implemented in 2009; silver eels are captured at former commercial fishing sites located in the upper Shannon and at Killaloe eel weir near the hydropower dams (Fig. 1). Silver eel trap and transport was initially developed on a pilot-scale basis at Killaloe in 2000, with a proportion (32–65%) of the commercial catch being released annually until 2005 (McCarthy et al. 2008). All eels captured at Killaloe since 2006 and at the upper Shannon sites since 2009 are transported and released to the unobstructed freshwater lower reaches, downstream of the hydropower dams.

Monitoring and sampling

The silver eel migration season on the River Shannon typically begins in September/October until the following January/February (Moriarty 1990; McCarthy et al. 2008), and herein is referred to by the

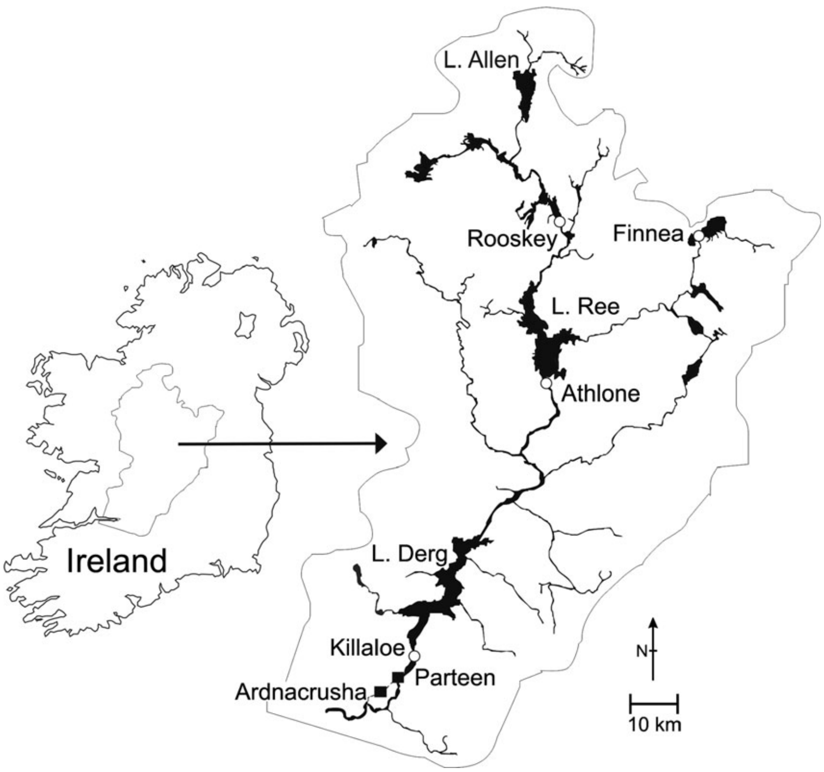

Fig. 1. The River Shannon catchment, with the three main lakes (Loughs Derg, Ree and Allen), conservation fishing sites (Killaloe, Athlone, Rooskey and Finnea) and hydropower dams (Ardnacrusha and Parteen) indicated.

year during which it begins (e.g., September 2010 to February 2011 is termed the 2010 season). At all fishing sites, nets are set from dusk until dawn, and are emptied regularly during the night to ensure captured eels are in optimal condition for inclusion in the trap and transport programme. Silver eel fishing operations were intensively monitored between 2008 and 2011, particularly at Killaloe eel weir. The eel weir (52°48′N 8°27′W), which is described in detail by Cullen & McCarthy (2000), is situated 3–11 km upstream of the hydropower dams (Fig. 1). Up to 20 stow nets are attached to the downstream side of a road bridge, either singly ($N = 1$) or in groups of three ($N = 5$) or four ($N = 1$), within seven of the bridge arches.

Representative samples of the catch were anaesthetised with clove oil and total-length was measured to the nearest 1 mm. Samples consisted of either the total catch when the nets were emptied, or the catch of specific sets of nets (i.e., the nets positioned within an arch of the bridge), depending on the intensity of migration. No significant difference in eel size was observed between night and morning net lifts (Mann–Whitney U-test: five sampling occasions, $N = 82$–283, all $P > 0.05$) or between eels captured from each arch (Kruskal–Wallis test: five sampling occasions, $N = 61$–494, d.f. = 6, all $P > 0.05$). Previous macroscopic examination of silver eel gonads on the River Shannon indicated that males do not exceed 430 mm and females <430 mm very rarely occur (McCarthy & Cullen 2000; MacNamara & McCarthy 2012). This criteria was therefore applied to length measurements to determine the sex ratio.

Silver eel production

Killaloe mark-recapture experiments

The silver eel population size at the lowermost fishing site (i.e., the silver eel run to Killaloe eel weir) was estimated annually (2008–2011) from mark-recapture experiments and catch analysis. For the mark-recapture experiments, silver eels were selected from the catch at Killaloe eel weir, anaesthetised and measured. Tagging was performed using external T-bar anchor tags (FD-68B; Floy Tag & Mfg. Inc., Seattle, WA, USA), which were inserted into the dorsal musculature, approximately 5 cm posterior to the origin of the dorsal fin. All tagged eels were allowed to recover sufficiently (minimum 2 h) prior to release. Tagged eels were divided into three equal subgroups and released from a boat ~200 m upstream of the eel weir (on the left, centre and right of the channel). All releases occurred after dark (typically 1800–2200 h), during periods when active silver eel migration had been confirmed by daily monitoring of eel weir catches. After each occasion that the nets were emptied, silver eel catches were carefully screened on a sorting tray for the presence of the conspicuous, fluorescent Floy tags, before being placed in the holding tanks. The suitability of external Floy tags for mark-recapture experiments at this fishing site was verified by comparison with identical handling and release protocols using internal Passive Integrated Transponders in 2009. No significant difference in recapture rate ($\chi^2 = 0.577$; d.f. = 1; $P > 0.05$) or size structure of recaptured eels (two–sample Kolmogorov–Smirnov test, $P > 0.05$) was found between methods.

Killaloe eel weir closure 2009

In 2009, extreme discharge (up to 843 $m^3 \cdot s^{-1}$) necessitated a 17 night closure of Killaloe eel weir during the peak migration period. As no catch data were available at the eel weir, a Dual Frequency Identification Sonar (DIDSON 300 m; Sound Metrics Corporation, Bellevue, WA, USA) was deployed 500 m upstream. This high-resolution multibeam sonar camera is capable of clearly observing objects in turbid and dark waters (http://www.soundmetrics.com/products/imaging-sonars/didson-300). Observations of passing eels were made during the time the nets would typically be set (i.e., 17:00–07:00 h) every 2–3 nights during the closure period (six nights in total). On each night, the DIDSON camera was positioned and operated identically [perpendicular to the flow; low frequency mode (1.1 MHz); set to 20 m range]. Analysis of DIDSON images was based on the number of eels observed during 20 min$\cdot$h^{-1} subsamples. To obtain a relationship between DIDSON counts and eel weir catches, further DIDSON observations were undertaken after fishing resumed at the eel weir in 2009 ($N = 3$ nights), although catches were low. Additional counts were possible during the peak migration in 2010 ($N = 7$ nights). The relationship between DIDSON eel counts and eel weir catches was examined using linear regression, and the DIDSON estimated catch during the eel weir closure was used to complete the population analysis in 2009.

Estimating silver eel population size at Killaloe

Silver eel population size at Killaloe was estimated using the unbiased modified Lincoln-Petersen method (Pollock et al. 1990). This required daily Killaloe catch (recorded in kg) to be converted to number of eels, taking account of possible seasonal variation in sex ratio and eel size (see Results). Length data sampled throughout each season were used to determine the sex ratio. Mean eel weight (male and female) was determined from this length data and the length–weight relationship given by MacNamara & McCarthy (2012). The number of eels was then calculated from the daily Killaloe catch, with the appropriate sex ratio and mean weights applied. Silver eel population size was estimated according to the formula:

$$P = \frac{(n_1 + 1) \times (n_2 + 1)}{(m_2 + 1)} - 1$$

where P is the population size, n_1 is the number of tagged eels released, n_2 is the total catch (in number of eels) and m_2 is the number of tagged eels recaptured. Standard deviation (SD) was estimated as:

$$\mathrm{SD} = \sqrt{\frac{(n_1+1) \times (n_2+1) \times (n_1 - m_2) \times (n_2 - m_2)}{(m_2 + 1)^2 \times (m_2 + 2)}}$$

Population size and standard deviation estimates were then converted back to biomass (kg) using the inverse of the procedure described above.

Total silver eel production

Killaloe population size estimates and upper Shannon catches [commercial fishery data in 2008 (17 fishing sites) and conservation fishery data in 2009–2011 (four fishing sites)] were combined to determine the silver eel production in the cascade catchment (herein termed *actual silver eel production*). Due to the operation of a commercial yellow eel fishery in 2008, it was necessary to take account of the removal of maturing yellow eels, which would have contributed to the silver eel production that season (i.e., 2008). The yellow eel fishery consisted of a series of fishing crews assigned to specific lakes in the catchment, fishing with either longlines or fyke nets. Each crew's total catch was obtained from official sales records. Male and female maturation curves for River Shannon eel populations, derived from Bevacqua & De Leo's (2006) DemCam model, were used to determine the proportion of the yellow eel catch that would have become silver eels that season (herein termed *potential silver eel production*). The DemCam model, like other demographic models (e.g., De Leo & Gatto 1995), assumes maturation to be a sigmoidal increasing function of size. For males, the proportion maturating was assumed to be 0 for eels <310 mm, 0.35 for eels 310–370 mm and 0.85 for eels 370–430 mm. For females, the proportion maturating was assumed to be 0.4 for eels 430–490 mm, 0.6 for eels 490–550 mm, 0.8 for eels 550–610 mm and 0.9 for eels >610 mm. Yellow eel length frequencies for each lake were obtained from a fishery-independent longline and fyke net monitoring survey in 2008, and were scaled to take account of the catch quantity for each gear type. The appropriate maturation rate was then applied to each length class to determine the potential silver eel component of the yellow eel catch. Actual and potential silver eel production were combined to give *total silver eel production* for the cascade catchment.

Retrospective silver eel production
Retrospective estimation of total silver eel production was undertaken for the 20-year period from 1992 to 2011. For actual silver eel production, the mean capture efficiency determined during the 2008–2011 mark-recapture experiments was assumed to be valid for Killaloe eel weir. Structurally, the eel weir has remained similar since being upgraded in 1982–1984 (McCarthy et al. 2008). During the 1990's, up to 34 nets were occasionally fished at the eel weir in times of very high catches, but this did not occur regularly, and these additional nets accounted for <10% of the daily catch (Cullen & McCarthy 2000). Since 2000, a maximum of 20 nets have been fished, as per 2008–2011. Potential silver eel production was estimated as described above, using official annual sales records, and yellow eel length frequencies from fishery-independent longline and fyke net surveys in 1995, 1998, 1999, 2000, 2003 and 2007. The intensity of the yellow eel fishery varied between 1992 and 2009, peaking at ~40 fishing crews in the late 1990's, to 20–25 crews in the mid 2000's.

Input–output model

Upstream migrating juvenile eels (glass eels and elvers) are trapped at main channel, tributary and estuarine sites below the cascade catchment, for stocking above the hydropower dams (Moriarty 1986; Quigley & O'Brien 1996; McCarthy et al. 2008). Natural recruitment to the cascade catchment (via the boat lock and fish passes at the hydropower dams) remains unknown, but is thought to be negligible compared to stocking (McCarthy et al. 2008). Count data (i.e., numbers·kg^{-1}) for each trapping site were used to determine the number of eels stocked annually since 1959. To account for age variation between trapping sites, all stocked eels were converted to year 0+ equivalents (e.g., year 3+ eels stocked in 2000 were included in the analysis as year 0+ eels stocked in 1997). Age data for each trapping site referred to the mean number of years spent in freshwater (Moriarty 1986; W. O'Connor, F. Egan & T.K. McCarthy unpublished data). Survival of stocked eels was considered to be a decreasing function of age, according to De Leo & Gatto (1995). Survival rate was applied to actual eel age rather than converted eel age. The relationship between the number of eels stocked and silver eel production was examined using linear regression. Time-lag intervals of up to 20 years were considered, corresponding to the age range of River Shannon silver eels reported by Arai et al. (2006). The last 3 years (2008–2011) of stocking data were excluded from the analysis as stocking data from these years were not complete, due to the conversion process described above.

Results

Population dynamics

Seasonal trends: sex ratio
The sex ratio of silver eel migrating via Killaloe was determined from length frequency analysis of representative catch samples in 2008 (N = 2729), 2009 (N = 1133), 2010 (N = 2026) and 2011 (N = 1527). In each year, the proportion of males decreased as the season progressed (Fig. 2). At the beginning of the migration season at Killaloe (October), male silver eels comprised 37.5–71.2% of the catch, but this decreased to <20% by February. The percentage of males in the catch (arcsine transformed) was significantly negatively correlated with sampling date during each year (2008, $r = -0.768$, $P < 0.001$; 2009, $r = -0.753$, $P = 0.031$; 2010, $r = -0.733$, $P = 0.016$; 2011, $r = -0.743$, $P = 0.022$). The annual sex ratio at Killaloe varied from 33.8 to 38.9% males. When upper Shannon catches were considered, the overall annual sex ratio varied from 18.4 to 24.2% males.

Seasonal trends: eel size
Length frequency analysis also revealed that in each year, the size of female silver eel migrating via Killaloe increased progressively during the season (Fig. 3). Female silver eel length data were not normally distributed (one-sample Kolmogorov–Smirnov test, all $P < 0.05$) and were therefore $\log_{10}$-transformed. Mean female silver eel length was significantly positively correlated with sampling date during each year (2008, $r = 0.553$, $P = 0.004$; 2009: $r = 0.776$, $P = 0.024$; 2010, $r = 0.760$, $P = 0.011$; 2011, $r = 0.809$, $P = 0.008$). No seasonal trend in male silver eel size was observed in any year (all $P > 0.05$). Monitoring at upper Shannon fishing sites was limited due to the shorter, more concentrated migration period, but no seasonal trend in female size was identified. Sex ratio or male eel size seasonal

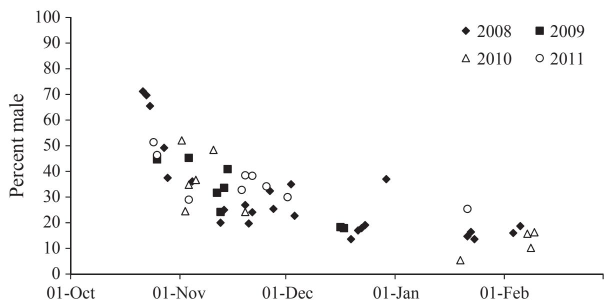

Fig. 2. Sex ratio of silver eels migrating via Killaloe, based on length frequency analysis in 2008 (2729 eels measured during 25 sampling occasions), 2009 (1133/8), 2010 (2026/10) and 2011 (1527/9).

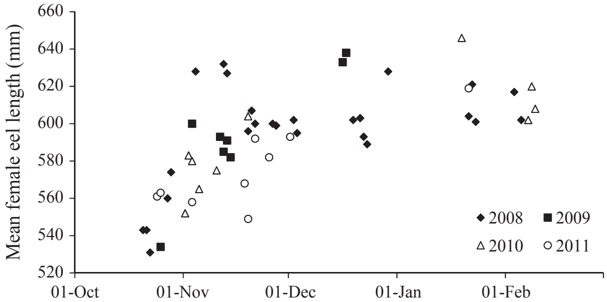

Fig. 3. Mean female total-length (mm) of silver eels migrating via Killaloe in 2008 (1867 eels measured during 25 sampling occasions), 2009 (785/8), 2010 (1291/10) and 2011 (919/9).

trends were not investigated in the upper Shannon, due to the predominance of females.

Silver eel production

Killaloe eel weir closure 2009

In 2009, no catch data were available for the 17 night closure of the eel weir (25 November to 11 December), and DIDSON eel counts were undertaken on six nights. Subsequently, during 2009 ($N = 3$ nights) and 2010 ($N = 7$ nights), the Killaloe catch–DIDSON count relationship was established, and is described by the regression equation:

$$\text{Killaloe catch (numbers)} = (1.6 \times \text{DIDSON eel counts}) + 20.9$$

($r^2 = 0.554$, $P = 0.014$, $N = 10$) (Fig. 4).

By applying the regression equation to the eel counts made during the eel weir closure, it was possible to estimate the eel weir catch on the six nights during which observations took place. The remaining nights were estimated by interpolation. These counts were converted to kg, which indicated that 3454 kg (10 035 silver eels) would have been captured at Killaloe eel weir during the 17 night closure period.

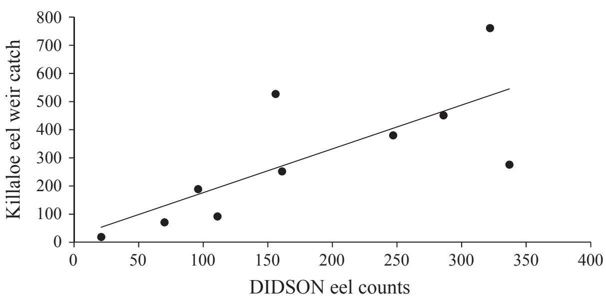

Fig. 4. Relationship between the number of eels captured at Killaloe eel weir and observed by DIDSON over 10 nights.

Killaloe silver eel population size

Killaloe catch was converted to number of silver eels, taking account of the seasonal trends described above. The number of silver eels captured at Killaloe (including the portion estimated by DIDSON in 2009) and population size estimates are shown in Table 1. Annual recapture rates were 20.8–25.0%, but did not differ significantly between years ($\chi^2 = 3.210$, d.f. = 3, $P > 0.05$).

Total silver eel production

Total silver eel production from the River Shannon cascade catchment was calculated based on Killaloe mark-recapture experiments, silver eel catch data from Killaloe and upper Shannon, DIDSON observations in 2009, and in 2008, potential silver eels removed by the yellow eel fishery (Table 2). In 2008, actual silver eel production was 57.3 t (1.35 kg·ha^{-1}). However, 28.8 t of yellow eels were removed during the summer fishery prior to this. From length frequencies and analysis of catches from specific lakes and gear types, this was estimated to include 18.3 t of potential silver eels. Therefore, total silver eel production in 2008 would have been 75.6 t, equal to 1.78 kg·ha^{-1} of wetted area. Actual silver eel production was estimated to be 68.6 t (2009), 62.7 t (2010) and 61.6 t (2011), equal to 1.62, 1.48 and 1.45 kg·ha^{-1} respectively. The 2009–2011 estimates represent total silver eel production, as no yellow eel fishing took place.

Table 1. Details of the mark-recapture and catch analysis at Killaloe: numbers of tagged eels released and recaptured; the estimated total number of eels captured at the eel weir; and the estimated population size (±SD) at Killaloe in numbers of eels.

Year	Released	Recaptured (%)	Killaloe catch	Population size	±SD
2008	635	151 (23.8)	36 663	153 409	10 797
2009	568	142 (25.0)	51 490	204 883	14 727
2010	394	95 (24.1)	41 912	172 454	15 217
2011	605	126 (20.8)	38 933	185 779	14 575

Table 2. Summary of the annual silver eel catch at Killaloe, population size at Killaloe, the upper Shannon catch and total silver eel production for the cascade catchment, with the estimated potential silver eels included for 2008 in parentheses.

Year	Killaloe catch (kg)	Population size at Killaloe (kg)	Upper Shannon catch (kg)	Total production (kg)
2008	10 472	40 653	16 698	57 333 (+18 254)
2009	15 452	55 585	12 999	68 584
2010	12 722	47 099	15 624	62 723
2011	10 712	46 049	15 501	61 550

Retrospective silver eel production

River Shannon silver eel production (actual and potential) and catch (yellow and silver eel) for 1992–2011 are shown in Fig. 5. A significant downward trend was not observed for actual silver eel production (Mann–Kendall test, $P > 0.05$), but was for total silver eel production (Mann–Kendall test, $P < 0.001$). Between 1992 and 2008, potential silver eel production represented 63.4–71.1% of the yellow eel catch, and between 1992 and 2011, the silver eel catch represented 26.5–55.3% of the total silver eel production (Fig. 5).

Input–output model

The number of eels stocked ($\log_{10}$-transformed) and total silver eel production (i.e., actual and potential) were significantly correlated when time-lag intervals of 10–18 years were applied, with the highest correlation coefficient obtained at 14 years. This relationship is described by the regression equation:

$$\text{Total silver eel production (t)} = (38.0 \times \log_{10}\text{number of eels stocked}) - 153.9$$

($r^2 = 0.773$; $P < 0.001$, $N = 17$).

This regression equation was used with stocking records to develop an input-output model to predict future total silver eel production. This model projects a significant downward trend in total silver eel production between 2012 and 2022 (Mann–Kendall test, $P = 0.002$), decreasing from 66.1 to 38.4 t (Fig. 6).

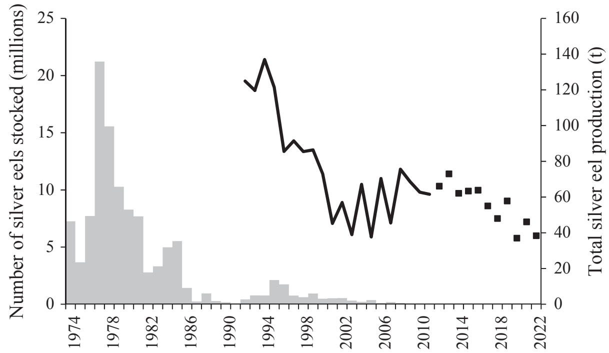

Fig. 6. Input–output model developed for the River Shannon (with 14-year time-lag), showing number of eels stocked (grey bars), total silver eel production (solid line) and predicted total silver eel production (squares).

Discussion

Population dynamics

Monitoring of silver eel migration between 2008 and 2011 revealed some interesting seasonal trends, specifically in relation to sex ratio and eel size. A higher proportion of male eels migrated earlier in the season on the River Shannon (Fig. 2), similar to the findings of Deelder (1970) in Lake Ijsselmeer, The Netherlands (see also Tesch 2003), Haraldstad et al. (1985) on the River Imsa, Norway and Todd (1981) for shortfin (*Anguilla australis*) and longfin (*Anguilla dieffenbachii*) eels in New Zealand. In Lough Neagh, Northern Ireland, Parsons et al. (1977) only observed early migration of male eels when the overall percentage of males was low (<25%). In terms of eel size, no seasonal trend was found for male eels, in contrast to Deelder (1970) and Parsons et al. (1977), but in agreement with Lobón-Cerviá & Carrascal (1992) for a male-dominated northern Spanish river. Female eels captured at Killaloe became progressively larger during the season (Fig. 3), an occurrence which has been noted previously by Haraldstad et al. (1985), Durif & Elie (2008) on the River Loire, France and by Jessop (1987) in Nova Scotia for American eels (*Anguilla rostrata*). During a previous study at Killaloe in the 1990's, neither sex ratio nor eel size seasonal trends were observed (McCarthy & Cullen 2000). In the 1970's and 1980's, Moriarty (1990) gave accounts of both seasonally increasing and decreasing eel size, but this referred to the entire River Shannon silver eel fishery, and no distinction was made between male and female eels.

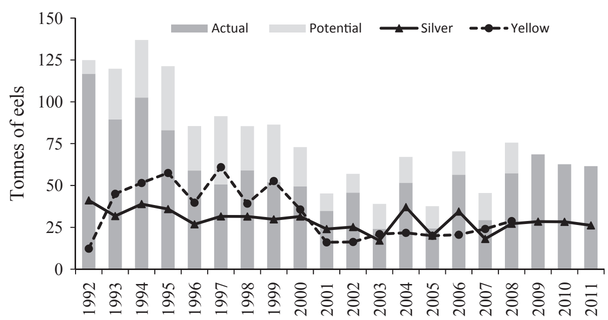

Fig. 5. Total silver eel production (actual and potential) and catch (yellow and silver eel) of the River Shannon (1992–2011). Note that the yellow eel fishery was closed after 2008.

Shifts in River Shannon eel population dynamics between previous studies (Moriarty 1990; McCarthy & Cullen 2000) and the present study are difficult to evaluate, due to the changing fishery management practices in the catchment. The currently observed migration trends on the River Shannon are often described as typical of anguillid eel populations (Tesch 2003), but it is likely that intensive removal of yellow eels and stocking of juvenile eels to upper Shannon lakes (Quigley & O'Brien 1996; McCarthy et al. 2008) may have obscured these patterns in previous years. Yellow eel fishing intensity and stocking levels have been declining since the mid 1990's, and in recent years, the former has ceased completely while the latter is negligible (no stocking to upper Shannon lakes; small quantities of juvenile eels are released above the hydropower dams and allowed to disperse naturally). Various anthropogenic impacts have been shown to affect eel population dynamics (e.g., McCleave & Jellyman 2004; Laffaille et al. 2006), but the natural density-dependant processes that regulate population structure and differential distribution of sexes are now occurring on the River Shannon (i.e., males predominate in lower catchment and females predominate in upper catchment), resulting in the sequential timing of arrival of male, smaller female and larger female silver eels at a given point.

The importance of understanding silver eel population dynamics has been highlighted by McCleave (2001), who demonstrated that small changes in population density and female length can have a greater impact on spawner escapement than different hydropower mortality rates in a highly regulated catchment. Due to the collapse in available stocking material and the recent conservation-orientated tendency for reduction or closure of eel fisheries (e.g., Cucherousset et al. 2007; DCENR 2008), similar population shifts to those described here may be anticipated elsewhere, such as the Irish River Erne, where intensive fishing and stocking formerly occurred (Matthews et al. 2003). Seasonal trends in silver eel migration should be accounted for in conservation actions (e.g., Durif & Elie 2008), such as the timing and duration of trap and transport, closed fishing season or controlled spillage, to maximise the benefit to large, highly fecund female eels (MacNamara & McCarthy 2012).

Silver eel production in the River Shannon

As an alternative to modelling, there have been some efforts in recent years to obtain empirical data on silver eel population size and production. Various habitat types have been investigated, including small (Acou et al. 2009; Bilotta et al. 2011) and large (Rosell et al. 2005; Klein Breteler et al. 2007; Winter et al. 2007) rivers catchments, marshes (Cucherousset et al. 2007) and lagoons (Amilhat et al. 2008; Charrier et al. 2012). In the present study, silver eel production was successfully estimated in a relatively large river catchment by integration of mark-recapture experiments, catch data and sonar observations. This production data refers to the area above the hydropower dams (cascade catchment), and does not include the main channel, tributaries or estuary further downstream (catchment area 3600 km^2). Electrofishing surveys indicate that relatively high densities of yellow eels (mostly male) are found in the freshwater lower reaches of the River Shannon (McCarthy et al. 2008). The estuary could also represent an important habitat for silver eels, due to higher growth rates in saline waters (e.g., Harrod et al. 2005) and the unobstructed seaward migration route. However, current eel management in this river basin district is primarily focused on the impact of the hydropower dams (DCENR 2008; McCarthy et al. 2008).

As Killaloe eel weir is the lowermost silver eel fishing site and adjacent to the hydropower dams, it was deemed a suitable location to undertake mark-recapture experiments. Over 99% of the lake and river area of the cascade catchment is located upstream of Killaloe. Silver eels for the mark-recapture experiments were selected from the trap and transport programme, and were therefore in optimal condition. All tagged eels were actively undergoing their seaward migration and had a silver appearance. Examination of various biological characteristics [eye and gonadosomatic indices in 2008 (MacNamara & McCarthy 2012) and eye and fin indices in 2009 and 2010 (McCarthy, T.K., Conneely, B. & MacNamara, R., unpublished data)] showed that silver eels captured at Killaloe were generally at an advanced maturation stage. In a recent telemetry study on the River Meuse (Verbiest et al. 2012), ~30% of silver eels settled after tagging despite being classified (by eye and fin indices) as migrants. However, as these eels underwent surgical transmitter implantation, their subsequent behaviour would not be considered comparable to eels that were externally Floy tagged, a much less invasive procedure. Furthermore, the riverine release location adjacent to the eel weir would reduce the tendency of tagged eels to delay migration compared to lacustrine release sites (McCarthy, T.K., Nowak, D., Grennan, J., Bateman, A., Conneely, B. & MacNamara, R., unpublished data). Therefore, nonmigration of tagged eels was not considered to be an issue in this study. The experimental protocols adopted, such as tagging with external Floy tags and use of the unbiased modified Lincoln-Petersen method, were shown to be appropriate at this location and have previously been used elsewhere in silver eel population analysis (e.g., Rosell et al. 2005; Klein Breteler et al. 2007; Winter et al. 2007). Although site specific to the Killaloe eel weir, the annual recapture rates (20.8–25.0%) are broadly similar to those obtained at an experimental eel weir on the River Erne (McCarthy, T.K., Nowak, D., Grennan, J., Bateman, A., Conneely, B. & MacNamara, R., unpublished data), but slightly lower than the Lough Neagh system, where two sequential eel weirs are in operation (Rosell et al. 2005). Together with hydropower mortality/route selection experiments and trap and transport releases, the mark-recapture data is essential for calculation of spawner escapement from the cascade catchment and as such, has been incorporated into Ireland's recent report to the European Commission on implementation of its EMPs.

Due to extreme discharge and the unanticipated temporary closure of Killaloe eel weir in 2009, it was necessary to rapidly develop an alternative monitoring technique at this location to complete the population analysis. This was achieved using a DIDSON, which has been used previously for observation and counting of various migratory fish species, including eel (Bilotta et al. 2011). Deployment of the DIDSON in the 1.5 km river stretch between Lough Derg outlet and Killaloe eel weir was limited to one suitable location. Eels were observed to a range of 20 m, and were readily identifiable by their elongated shape and distinctive swimming/locomotion. Large debris, such as branches, are seldom found in the nets at Killaloe, and hence, misidentification was not an issue. Despite the river width (~180 m) and the relatively small percentage of the water column being insonified (5–7% depending on water level), a significant relationship was obtained between DIDSON counts and Killaloe catch (Fig. 4). On the narrower and more uniform Lower River Erne in Northern Ireland, where ~18% of the water column was insonified, a more robust DIDSON–catch relationship was obtained (McCarthy, T.K., Nowak, D., Grennan, J., Bateman, A., Conneely, B. & MacNamara, R., unpublished data). Remote eel counting methods, such as hydroacoustics, have proven to be very useful (e.g., McCarthy et al. 2008), and the use of DIDSON to accurately quantify silver eel migration represents a significant addition to currently available population analysis tools. However, one point that should be noted is that even though the catch at Killaloe was successfully estimated in 2009, the recapture rate of tagged eels may have been slightly higher during this season, as silver eels were only observed by DIDSON during the closure period, rather than the catch being physically screened for tags. If some tagged eels migrated undetected during the closure period, the estimated population size and production would have been slightly lower for this year.

To fully quantify silver eel production prior to 2009, it was necessary to calculate the proportion of the yellow eel catch that comprised potential silver eels. This was carried out using the maturation curves developed specifically for River Shannon eels by Bevacqua & De Leo (2006). On the River Shannon, 430 mm total-length can be used to reliably distinguish males and females after transformation to the silver eel life-stage (McCarthy & Cullen 2000; MacNamara & McCarthy 2012). However, as sufficient histological data were not available for yellow eels, we relied on yellow eel length frequencies to assign the appropriate maturation rate. While that this may have lead to misclassification of some females as males (i.e., yellow eels <430 mm may be females that will continue growing for a number of years), we believe that this was most likely minimal. Where available, comparisons of potential silver eel sex ratios from specific lakes with those of the silver eel catch at the outlet were very similar. No minimum size limit was enforced on the River Shannon, but small yellow eels were generally returned by fisherman due to their low market value. In the uppermost Shannon lakes (e.g., Loughs Sheelin, Ennel, Derrevaragh), yellow eels >430 mm comprised the bulk of the catch (e.g., Arai et al. 2006; Yokouchi et al. 2009). Further downstream in Lough Derg (Fig. 1), the proportion of yellow eels <430 mm that were captured was higher, and this is reflected by the higher percentage of male silver eels at the lake outlet (Killaloe).

Silver eel production in 2008 was 57.3 t, but if no yellow eel fishing had occurred during that year, it is likely that it would have been 75.6 t. Following EMP-specified closure of the yellow eel fishery, silver eel production increased to 68.6 t in 2009, but decreased again to 61.6 t by 2011. This is considerably lower than the EMP-estimated current production of 85.7 t (DCENR 2008). Annual fluctuations in silver eel production have occurred, particularly during the 2000's (Fig. 5 and 6) and may be attributable to a variety of causes (e.g., stocking levels, fishing intensity and environmental conditions). Robinet et al. (2007) suggested that during years with unfavourable environmental conditions, not all silver eel may migrate. Likewise, during years of exceptional conditions, maximum silver eel migration may occur. In 2009, high numbers of silver eels migrated, possibly reflecting the high discharge levels favoured during migration (Tesch 2003), but also the fact that there was no removal of potential silver eels by a yellow eel fishery. The benefit of yellow eel fishery closure to silver eel production in 2009 was clearly apparent, with an increase from 2008 of over 11 t. However, as the input–output model suggests, silver eel production in the river looks set to continue declining, due to the collapse in recruitment (Fig. 6). The model, similar to those developed by other authors (e.g., Parsons et al. 1977; Vøllestad & Jonsson 1988; Allen et al. 2006) offers a baseline for management of eel stocks on the River Shannon over the coming decade. The composite structure of River Shannon eel subpopulations resulted in significant correlations between input and output being obtained for time-lag intervals of 10–18 years, corresponding to the silver eel age range in the catchment (Arai et al. 2006). A predictive model based on input in numbers and output in biomass is problematic (Allen et al. 2006), due to population structure shifts associated with a declining population, changing fishery management practices and other compensatory factors (e.g., Parson et al. 1977; this study). However, as continuing assessment on the River Shannon is undertaken, this preliminary model can be improved annually.

Overview of silver eel production

To facilitate comparisons with other studies, annual silver eel production on the River Shannon from 2009 to 2011 is expressed in terms of wetted area (1.5–1.6 $kg{\cdot}ha^{-1}$). However, differing productivity potential of, e.g., lake habitat versus river habitat (Oliveira et al. 2001) or shallow zones versus deep zones (Yokouchi et al. 2009), may bias this measurement (see also Acou et al. 2009). Nonetheless, assuming equal productivity potential of all areas, the River Shannon is comparable with other Irish rivers, such as the Erne (1.6 $kg{\cdot}ha^{-1}$; McCarthy, T.K., Nowak, D., Grennan, J., Bateman, A., Conneely, B. & MacNamara, R., unpublished) and the Burrishoole (1.3 $kg{\cdot}ha^{-1}$; R. Poole personal communication; see also Poole et al. 1990), whereas silver eel production is higher (4–4.6 $kg{\cdot}ha^{-1}$; Rosell et al. 2005) in Lough Neagh, primarily reflecting the long-term intensive glass eel stocking programme (Parsons et al. 1977; Rosell et al. 2005).

Elsewhere in Europe, recent field data is relatively scarce. In two Mediterranean lagoons in southern France, Bages-Sigean (3800 ha) and Or (3170 ha), silver eel production was estimated to be 30–34 $kg{\cdot}ha^{-1}$ (Amilhat et al. 2008) and 13.2 $kg{\cdot}ha^{-1}$ (Charrier et al. 2012) respectively. In western France, Acou et al. (2009) estimated silver eel production from two small coastal catchments, the Oir (87 km^2) and the Frémur (60 km^2), to be 2.4–6.3 and 4.7–26.8 $kg{\cdot}ha^{-1}$ respectively. However, the latter assumes that stream eel densities are not applicable to reservoirs, which represent 91.2% of the Frémur's wetted area. If the stream densities of silver eels are applied to the total wetted area (60 ha), production was 0.6–3.3 $kg{\cdot}ha^{-1}$. In the Brière marsh (~600 ha aquatic habitat) in western France, silver eel production was estimated to be 3.5–9.1 $kg{\cdot}ha^{-1}$ in a freshwater protected area, but was generally lower (1.0–4.8 $kg{\cdot}ha^{-1}$) in adjacent fished zones (Cucherousset et al. 2007). Bilotta et al. (2011) estimated silver eel production in the River Huntspill in southern England to be ~6 $kg{\cdot}ha^{-1}$.

Despite the relatively low silver eel productivity in Ireland compared to elsewhere in Europe, it is important to consider the reproductive contribution of the silver eels produced. Spawner quality issues, such as the effect of contaminants on egg development (e.g., Palstra et al. 2006) or the small size/low fat content of silver eels (Clevestam et al. 2011), may be a major factor in the eel decline. In general, little or no contamination occurs in Irish eel populations (McHugh et al. 2010). Due to the low density, many Irish rivers produce female dominated silver eel populations, with a high proportion of large individuals (Poole et al. 1990; McCarthy & Cullen 2000; Rosell et al. 2005; Yokouchi et al. 2009; this study). As fecundity in eels is size-related (MacNamara & McCarthy 2012), the population fecundity of River Shannon silver eels is likely to be high. Based on the size–fecundity relationship given by MacNamara & McCarthy (2012), and length frequency/sex ratio data presented here, the number of eggs produced annually (2009–2011) on the River Shannon was determined to be $1.69–2.12 \times 10^{11}$. This approach to calculation of the reproductive contribution of a river accounts for the relative importance of large female eels. In contrast, silver eel production in the Bages–Sigean lagoon is almost double (114.3–128.5 t; Amilhat et al. 2008) that of the River Shannon. However, egg production in Bages-Sigean is just $3.04–3.42 \times 10^{10}$, due to the male (97%) predominance. In this regard, the River Shannon compares favourably with more productive waterbodies, and represents an important source of spawners.

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