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Is proximity to the North Atlantic Drift and the Continental Shelf Current sustaining freshwater European eel populations in western Scotland?

COLIN E. ADAMS*, JASON D. GODFREY†, JENNIFER A. DODD* AND PETER S. MAITLAND‡

*Scottish Centre for Ecology and the Natural Environment, University of Glasgow, Glasgow, Scotland

†Freshwater Laboratory, Marine Scotland Science, Pitlochry, Scotland

‡Fish Conservation Centre, East Lothian, Scotland

SUMMARY

1. We report on freshwater resident eel numbers in western Scotland based on two time series of data, independent of each other, spanning 28 years and that do not rely upon fisheries information.
2. Data from eel captures on trash screens of a pumping station (1982–2003) on Loch Lomond and electrofishing data from a stream in Lochaber, the Allt Coire nan Con (1989–2010), are compared with similar time series eel population data from elsewhere in the British Isles and more widely in Europe.
3. Over the period of the study, indices of eel numbers from across Europe declined by between 72 and 95%; in stark contrast, neither time series from western Scotland showed evidence for decline between 1982 and 2010.
4. We provisionally conclude that freshwater populations in western Scotland are being maintained by regional processes directly related to the proximity of the leading edge of the North Atlantic Drift and the Continental Shelf Current and the direction of prevailing winds.

Keywords: *Anguilla anguilla*, population dynamics, recruitment

Introduction

There are strong indicators that many populations of the European eel [*Anguilla anguilla* (L.)], an important component of freshwater ecosystems across Europe, are 'outside safe biological limits' (E.U., 2007). Multiple, independent, long-term data series, mostly from populations that are exploited, show considerable consistency across a number of life-cycle stages and across a broad geographic area in Europe (ICES, 2008, 2010). Data collated by the International Council for the Exploration of the Sea (ICES), for example, show that average glass eel recruitment to fisheries across Europe has declined by around 98% over three decades (ICES, 2008, 2010). Similarly, data show declines in the population size of migrating yellow eels of 92% and landings of yellow eels from commercial fisheries of ca. 73% over the same period (ICES, 2008). Estimates of the effective population size of the European eel from the North Atlantic, Baltic and North Sea areas, derived from analysis of genetic variation, suggest that the population may be as low as 6000 individuals (Wirth & Bernatchez, 2003).

Numerous explanations have been advanced for this decline, including changes in ocean climate, overexploitation, the impact of a recently introduced nematode parasite (*Anguillicoloides crassus*, Kuwahara, Niimi & Itagaki 1974), reduction in habitat quality and quantity, pollution and mortality during passage through hydropower turbines (Starkie, 2003). None of these explanations is mutually exclusive, and compelling evidence for any playing a direct role is absent (Starkie, 2003). Even whether the origin of the decline is the result of freshwater, inshore or oceanic influences remains unclear. The spatial variation in the age at which eels mature across

Correspondence: Colin E. Adams, Scottish Centre for Ecology and the Natural Environment, University of Glasgow, Rowardennan, Glasgow G63 0AW, Scotland.
E-mail: colin.adams@glasgow.ac.uk

Europe complicates population models, and the panmictic nature of the stock means that local effects are not directly coupled to subsequent recruitment. Nevertheless, the continuing decline in recruitment to the freshwater populations on a European scale now means that local populations may continue to decline even where human-induced mortality is reduced to zero (Åström & Dekker, 2007).

In the European context, western Scotland presents a relatively pristine habitat for eels. The region has not suffered from a widespread decline in water quality, or habitat disruption, nor have there been profound changes in accessibility or any sustained commercial exploitation of eel populations. In addition, the swim bladder parasite *Anguillicoloides crassus* has not been reported from the region (Defra, 2010). There is, however, a paucity of published historical data on eel populations in this region. We therefore examined long-term change in freshwater eel populations in western Scotland using two data sets comprising measures of eel standing stock, independent of each other and not reliant upon fisheries information, spanning a period of 28 years, in two contrasting catchments on the west coast of Scotland. The first is from 1982 to 2003 for Loch Lomond, a large freshwater lake, and the second is from 1989 to 2010 for a small upland stream, the Allt Coire nan Con.

Methods

Fish are entrained at a pumping station at Ross Priory, on the south shore of Loch Lomond, west-central Scotland (056°3′N, 004°33′W). Water is drawn from the lake through an intake 229 m from the lake margin and 2.6 m below its lowest recorded level. After passing through cowls, which reduce the formation of vortices, the water is drawn through two 1.7-m-diameter pipes to a coarse screening chamber. Water is then passed through mechanically operated, rotating, 8-mm mesh, band screens before being chlorinated and pumped for additional treatment elsewhere. Fish, along with other debris (mostly filamentous algae and unattached macrophytes), are trapped on the band screens and washed into large baskets of the same mesh. From late 1981 onwards, fish have been removed daily from the screens and stored in formalin. They are subsequently washed, sorted, identified and counted on a monthly basis (Adams & Maitland, 1998; Devine, Adams & Maitland, 2000).

Over the study period, 130 617 individuals from 17 species of fish have been recorded by this capture method. Four fish species were recorded regularly comprising 99.7% of the catch; these are eel, three-spined stickleback (*Gasterosteus aculeatus* L.), perch (*Perca fluviatilis* L.) and ruffe [*Gymnocephalus cernuus* (L.)]. The long-term changes in ruffe and three-spined stickleback have been examined elsewhere (Adams & Maitland, 1998; Wootton, Adams & Attrill, 2005, respectively). Here, the long-term change in eel numbers is examined in detail. In 2004, the requirement for potable water from this site changed markedly, which resulted in a dramatic reduction in the pumping rate. As a result, the number of fish entrained also reduced dramatically from an annual mean of 5937 individual fish to only a few dozen. Thus, here only data from the 22-year period between 1982 and 2003 (inclusive) are analysed.

The second data series from the Allt Coire nan Con, a small stream in Lochaber, derives from electrofishing surveys conducted at two sites (056°45′N, 005°36′W) by Marine Scotland Science as part of the Acid Water Monitoring Network, between 1989 and 2010. Each site was surveyed by electrofishing once each year in September or October using stop nets and three separate passes, targeting all species present (Atlantic salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.) and eels). Eels were anaesthetized using MS222 and measured (length). Depletion method estimates of population size (Zippin, 1958) could not be calculated for eels, because of a lack of depleting numbers with successive sampling, so the total numbers caught over the three survey passes was used as an estimate of population size.

The ICES has collated time series data on a range of indices of eel abundance across Europe (ICES, 2008). To enable a comparison of trends in these data with those from western Scotland, the following four data sets providing insights into eel abundance spanning a similar time period are analysed further.

1. The total reported yellow and silver eel fishery landings data for 17 European countries (from 1982 to 2005, the last year for which full data are available (ICES, 2008).

2. The recruitment of glass eels to the freshwater eel population, measured as a mixture of trapping surveys and commercial catches from 22 rivers in 12 countries (Belgium, Denmark, England, France, Germany, Italy, the Netherlands, Northern Ireland, Portugal, Republic of Ireland, Spain and Sweden) from 1982 to 2008 (the last year for which full data are available) (ICES, 2008). Recruitment is measured as a geometric mean of all reporting rivers and presented as deviations from the average of 1979 to 1994 (scaled to equal 100).

3. The recruitment of yellow eels into freshwater populations in 10 rivers in five Northern European countries (Belgium, Denmark, Ireland, Norway and

Sweden) from 1982 to 2008, the last year for which full data are available (ICES, 2008). Recruitment is measured as the geometric mean of the means of all reporting rivers from within each country presented as deviations from the average of 1979 to 1994 (scaled to equal 100).

4. The recruitment of glass eels and young of the year to freshwater populations in the British Isles from 1982 to 2008, the last year for which full data are available (ICES, 2008), comprising an index of juvenile eels (from combined commercial catches and trapping) from five sites in the Republic of Ireland, Northern Ireland and England, presented as deviations from the average recruitment from 1979 to 1994 data (indexed as 100).

To look for trends in indices of eel population size over the study period, a general linear model (GLM) was used. To look for trends in eel indices within the study period at the two study sites examined here, a generalised additive model (GAM) approach was taken. All statistical analyses were executed through R (R Development Core Team, 2011).

Results

European eels were recorded in catches at the Ross Priory Pumping Station, every year between 1982 and 2003. The 22-year mean (±SD) annual catch was 112 ± 138 individuals (range 2–524). A sample of 49 eels taken in the years 1982–85 had a mean (±SD) length of 28.0 ± 9.7 cm (range 15.3–64.6 cm). Pump rate at Ross Priory also varied across the 22-year period with a mean of 75 209 million L per annum (±12219 SD; range 46 273–105 479 million L p.a.). Across all years, annual pumping rate significantly predicted annual catches of eels (regression of $\log_{10}$-transformed annual eel catch on $\log_{10}$-transformed annual pump rate $F_{1,21} = 19.9$; $P = 0.0002$; Fig. 1). To correct for the effect of variable sampling effort on catch rate, residuals of annual catch on annual pump rate derived from the catch on pump rate regression (Fig. 1) were calculated.

To look for a change in eel population size over the 22-year time series, eel catch rate ($\log_{10}$-transformed) corrected for sampling effort (residuals) was regressed on year. Effort-corrected eel capture rate (residuals) were not predicted by year ($F_{1,21} = 2.10$, $P = 0.16$; Fig. 2). GAM analysis did not show any evidence of significant cycling in the data within the 22-year study period for Loch Lomond (GAM model fitting explained = 9.5% of variation, $P = 0.162$).

At the Allt Coire nan Con, there was a high degree of coherence between the two survey sites amongst years (Pearson's R, 0.71, d.f. = 21, $P < 0.001$), so data from both sites were combined in a single analysis. The mean (±SD) annual number of eels caught was 69.2 ± 33.3 (range 13–170). There was no significant linear trend (linear regression, $F_{1,20} = 2.21$, $P = 0.15$) between year and total numbers caught, although there were both very low and very high values in the first 3 years of the study (Fig. 3). GAM analysis showed evidence of significant cycling in the data within the study period for Allt Coire nan Con (GAM model fitting explained = 57.1% of variation, $P < 0.0001$; Fig. 4).

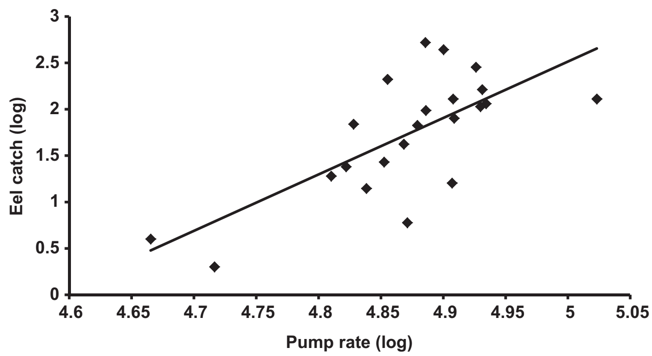

Fig. 1 Eel numbers ($\log_{10}$-transformed) captured in the Ross Priory Pumping Station each year regressed on annual pumping rate ($\log_{10}$-transformed) ($P = 0.0002$).

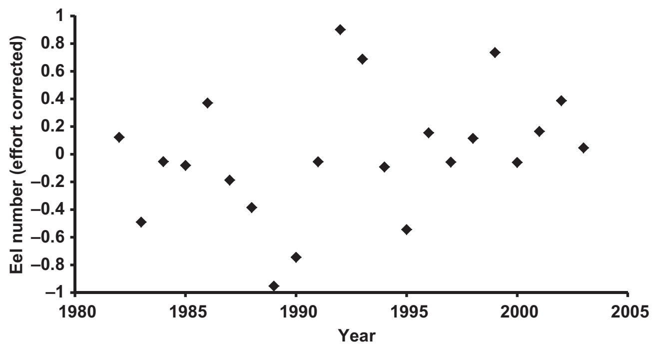

Fig. 2 Effort-corrected (residuals) annual eel catches at Loch Lomond over 22 years from 1982 to 2003.

Over the study period, the mean (± SE) annual mean eel length was 17.5 ± 0.02 cm (range 15.9–20.2 cm). Mean eel length declined significantly over time ($F_{1,20} = 9.90$, $P = 0.005$, $r^2 = 0.33$, $b = -0.092$; Fig. 5), whilst skewness increased over the time period ($F_{1,20} = 5.17$, $P = 0.034$, $r^2 = 0.20$, $b = 0.03$). These two relationships indicate that the proportion of smaller eels in the population increased over the time period of this study, indicating strong recruitment of younger age classes to the population.

In contrast, commercial eel fishery catches from across Europe show a different pattern. Total combined eel fishery landing statistics from 17 countries from between

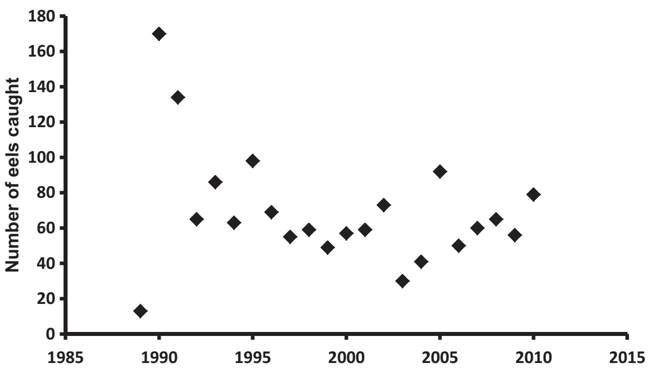

Fig. 3 Combined numbers of eels caught annually during electrofishing sampling at two sites on the Allt Coire nan Con, 1989–2010. There is no significant temporal trend ($P > 0.2$).

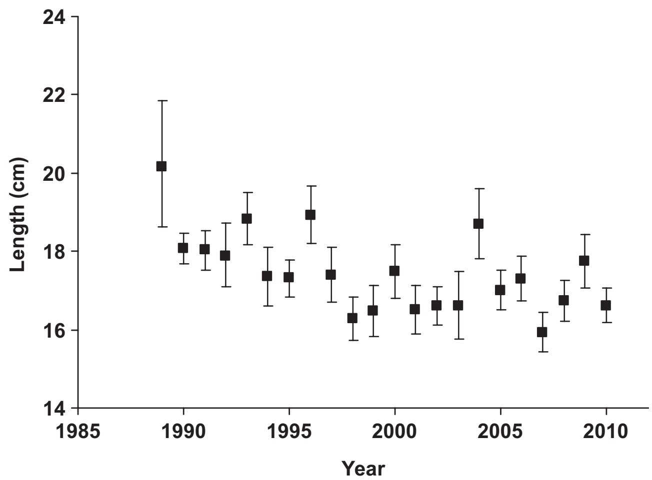

Fig. 5 Mean length of eels electrofished in the Allt Coire nan Con (upper and lower sites combined) from 1989 to 2010; error bars show standard errors. Mean length decreased significantly over time ($P < 0.01$), whilst skewness increased significantly ($P < 0.05$).

1982 and 2005 (source ICES, 2008) show a strong and negative trend with time (Fig. 6a, linear regression; $F_{1,23} = 681$, $P < 0.00001$, $r^2 = 0.97$, $b = -416$, intercept = 837821). This linear model indicates a decline in catches of 72% over the period 1982–2005.

The $\log_{10}$ -transformed, geometric mean of glass eel recruitment to fresh water for 22 index rivers from 12 countries across Europe over the 27 years (1982–2008) also shows evidence of a strong negative trend with time (Fig. 6b, linear regression, $\log_{10}$ -transformed; $F_{1,26} = 533$, $P < 0.00001$, $r^2 = 0.95$, $b = -0.050$, intercept = 103). This linear model indicates a decline in glass eel recruitment of 95% over the period 1982–2008.

The geometric mean yellow eel recruitment ($\log_{10}$-transformed) for 10 index rivers from five Northern European countries (Belgium, Denmark, Ireland, Norway and Sweden) over the 27-year period examined here is shown in Fig. 6c. Linear regression shows a strong negative decline in yellow eel recruitment ($\log_{10}$-transformed) to freshwater eel populations over this time ($F_{1,26} = 127$, $P < 0.0001$, $r^2 = 0.83$, $b = -0.035$, intercept = 71.1). This linear model indicates a decline in recruitment of 88% over the period 1982–2008.

In the British Isles, recruitment to freshwater populations measured by commercial catches of glass eels and juvenile trapping from five sites in the Republic of Ireland, Northern Ireland and England also declined over the period covered by this study (Fig. 6d). Between 1982 and 2008, the recruitment index fell from 179 to 1 (data derived from ICES, 2008). A linear regression model shows that year is a very strong predictor of $\log_{10}$-transformed recruitment index data ($F_{1,26} = 33.3$, $P < 0.0001$, $r^2 = 0.55$, $b = -0.043$, intercept = 86.0) and that over the study period, juvenile recruitment declined by around 92%.

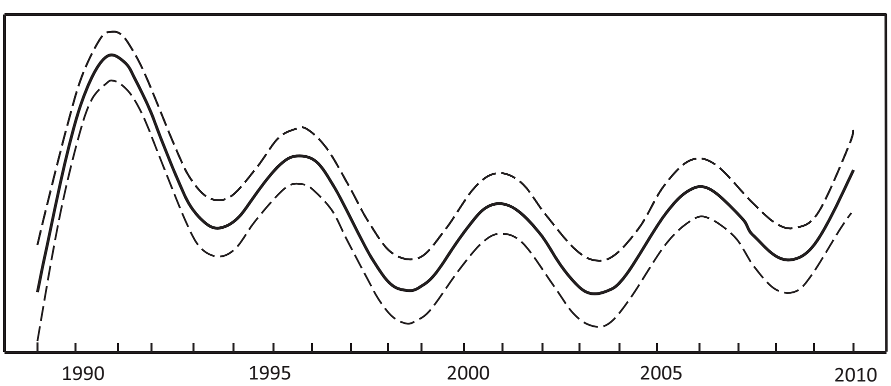

Fig. 4 Generalised additive model (GAM) analysis of eel catches by electrofishing between 1989 and 2011 from Allt Coire nan Con. Shown is the smoothing function (solid line) on year ±2 standard deviations (broken line) (GAM fitting explained = 57.1% of variation, $P < 0.0001$).

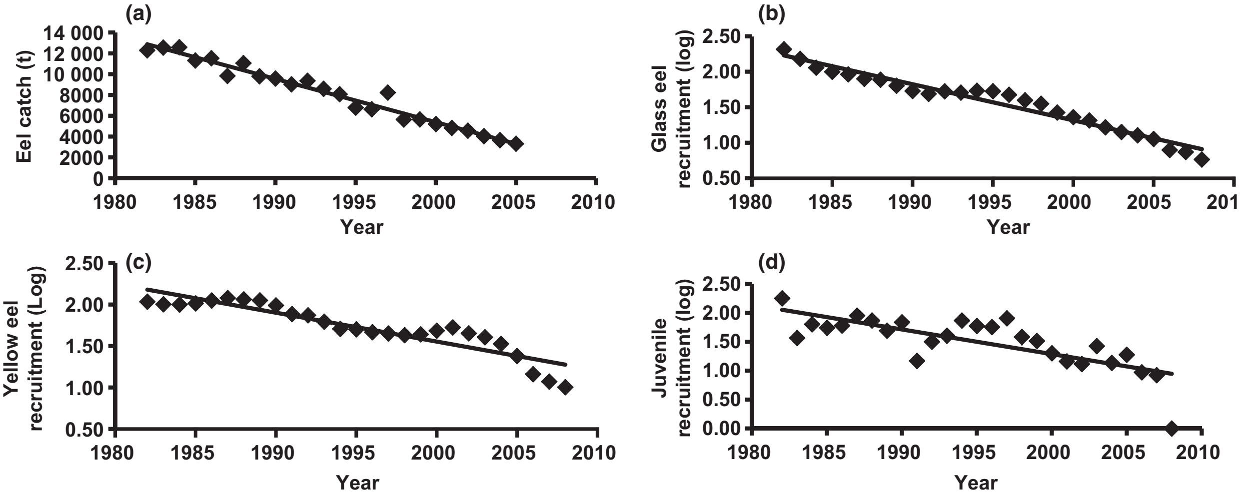

Fig. 6 (a) The total combined reported eel fishery landings (tonnes) from 17 countries (1982–2005) ($P < 0.001$). (b) The geometric mean index of glass eel recruitment ($\log_{10}$-transformed) (commercial catch data) to fresh water for 22 index rivers from 12 countries across Europe (1982–2008) ($P < 0.001$). (c) The geometric mean index of yellow eel migration into fresh waters ($\log_{10}$-transformed) in five Northern European countries for 10 index rivers ($P < 0.001$).(d) The geometric mean of recruitment of eels ($\log_{10}$-transformed) (glass eels and young of the year) to fresh waters in the British Isles (commercial catch and survey data) (1982–2008) (data from five sites in England, Republic of Ireland and Northern Ireland) ($P < 0.002$). Data source: ICES (2008).

Discussion

A number of strands of evidence from a range of independent data sources point towards a conclusion that eel numbers have declined significantly, rapidly and to very low levels and that this decline has been consistent over many years and generally widespread across Europe (Dekker, 2008). This evidence has lead to the conclusion that freshwater eel populations are 'outside safe biological limits' (E.U., 2007).

Over the period covered by the study presented here, total reported eel landings from fisheries in 17 European countries declined by around 72% and glass eel recruitment from 22 rivers in 12 countries by 95% (Fig. 6 a,b; ICES, 2008). Whilst fisheries data alone are not necessarily a reliable indicator of population size changes (de Mutsert *et al.*, 2008), indices of change which are not wholly dependent on fishery data appear to show a similar trend. Yellow eel migration into fresh waters in five North European countries dropped by 88% between 1982 and 2008 (Fig. 6c; ICES, 2008). Similarly, data only partially dependant on fisheries from the British Isles (England, Republic of Ireland and Northern Ireland, but not Scotland) show a decline of 92% in juvenile recruitment to freshwater populations over the same period (Fig. 6d; ICES, 2008). Elsewhere, a number of studies not reliant upon fishery data have shown significant declines in eel numbers. Long-term fyke trapping surveys showed an approximately fivefold reduction in two size classes of eels between ca. 1984 and 2010 in the Wadden Sea (van der Meer, van der Veer & Witte, 2011). A long-term study of eels entrained in a power station cooling water intake on the Severn Estuary, England (Henderson *et al.*, 2012), showed a 15% decline per annum in eel numbers between 1981 and 2009. Bark, Williams & Knights (2007) reported declines in eel numbers in scientific surveys in four rivers in south-east England between 1984 and 2005 and from the River Piddle in southern England from 1977 to 2003. In western Ireland, silver eel migration from the Burrishoole system declined markedly between 1959 and 1988 (although there is some evidence of a later recovery) (Poole, Reynolds & Moriarty, 1990). In contrast, the evidence of the study presented here is that the size of the freshwater eel populations of the two unconnected fresh waters examined has not declined over the last three decades. This long-term pattern of population change is diametrically opposed to that generally reported from elsewhere in Europe.

It is highly unlikely that slow growth and delayed seaward migration is masking declining populations at the two relatively northerly sites reported here. Although both slow growth (ca. 13 mm per year in an upland stream [a tributary of the River Dee, North-East Scotland) (Chadwick *et al.*, 2007)] and old age (51 years from a lake in the Outer Hebrides (Williamson, 1976) have been recorded in Scotland, relatively few lake eels are older than 30 years of age (<7% of eels were found to be >30 cm, Williamson, 1976). Conversely, the small mean size of eels from Loch Lomond suggests relatively young individuals form the bulk of fish sampled from this site.

Eel numbers from Allt Coire nan Con show a temporal decline in the mean length and an increase in skewness, consistent with an increasing, rather than a decreasing, rate of recruitment to the freshwater population. There was also evidence of an approximate 5-year cycle of periodicity in abundance of sampled eel within the study period at Allt Coire nan Con (but not at Loch Lomond). There is no obvious explanation for the apparent 5-year cycling in Allt Coire nan Con.

Eels are widespread in their distribution in Scotland and particularly so in western drainages (Shafi & Maitland, 1972; Defra, 2010). Although there is a paucity of robust, long time series data on eels from elsewhere in Scotland to determine with certainty the broader pattern across the country, there is some limited evidence that freshwater eel population stability extends beyond these two populations.

Incidental eel captures during electrofishing surveys (for other species) in Scotland from between 1997 and 2005 provide evidence, at least for some areas (notably western Sutherland, north-west Scotland) for a marginal increase in numbers of yellow eels in streams over this period (May & Marshall, 2008; Defra, 2010). In Lochaber, western Scotland, a recent electrofishing survey of eels at 80 sites in 11 catchments found no evidence for a contraction in the distribution of eels in the area and no evidence of consistent change in eel numbers over the period 1996–2010 (Baum & Smith, 2010). A recent study on the Isle of Mull, western Scotland (Goldspink *et al*., 2009), showed very high densities of elvers recruiting to fresh water there. Similarly in south-west England, Bark *et al*. (2007) reported stable eel numbers in the upper tributaries of the Severn catchment between 1983 and 2004.

Thus, there is some evidence that the long-term stability of the eel populations in western Scotland reported here is indicative of a broader trend of eel population stability in the fresh waters of western Scotland and possibly elsewhere in the western U.K. What is less evident are the mechanisms that may be promoting this stability here, which appear to be absent from elsewhere in Europe.

One possibility is that recruitment into freshwater populations in western Scotland has declined but that this is not reflected in long-term change in population sizes. Acou *et al*. (2011) and Lobón-Cerviá & Iglesias (2008) have both recently shown that eel populations of the River Fremur (Brittany) and the Rio Esva (north-west Spain), respectively, have remained stable, despite a decline in recruitment to fresh water, as a result of density-dependant mortality. The increasing proportion of small eels in the Allt Coire nan Con population indicates that recruitment to this population most likely increased between 1989 and 2010, whilst population density has remained constant. Thus, at least for this population, it is unlikely that reduced freshwater recruitment and consequential reductions in density dependant mortality can explain long-term population stability.

Another possible explanation may be the absence of the non-native, pathogenic, parasitic nematode that infects the swim bladder of eels. *Anguillicoloides crassus* was introduced to Europe from East Asia in the 1980s and is now widespread in mainland Europe, as well as England and Wales. It is known to be present in three catchments of eastern Scotland (Lyndon & Pieters, 2005; Marine Scotland Science, unpublished data), but has not yet been reported in western Scotland. Evidence of a population regulation effect by this parasite on eels is scant (Bernies, Brinker & Daugschies, 2011), and so this mechanism only provides a potential partial explanation of the results presented here.

A more plausible explanation may be that the geographic position of western Scotland results in a pattern of recruitment into the freshwater populations that is different from elsewhere. Although there has been debate about the reliance of larval eels on oceanic currents as opposed to active swimming during migration across the Atlantic (Schmidt, 1923; Lecomte-Finiger, 1992, 1994; McCleave *et al*., 1998; Tesch, 2003; Bonhommeau *et al*., 2009), it appears most likely that larval eels approach the continental shelf of Europe by passive migration using the Gulf Stream and its extension the North Atlantic Drift (Fig. 7) (Knights, 2003; Kettle & Haines, 2006; Bonhommeau, Chassot & Rivot, 2008) and that they metamorphose to

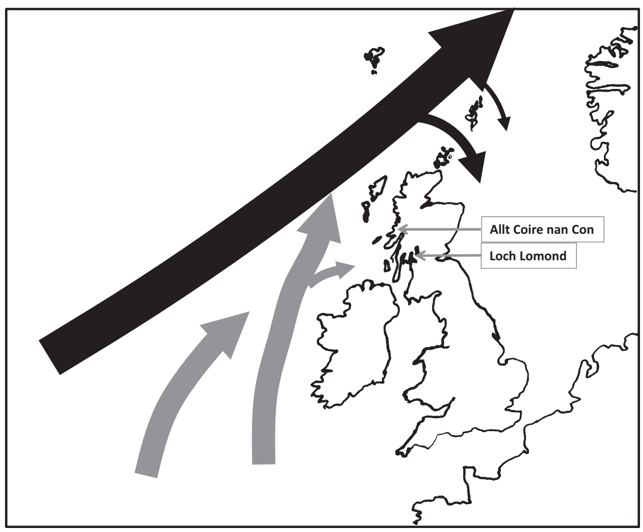

Fig. 7 The major near-shore currents adjacent to the western U.K. Black arrows indicate the direction of the North Atlantic Drift and grey the Continental Shelf Current (derived from Reid *et al*., 1997 and Malcolm *et al*., 2010).

glass eels at, or shortly before, reaching the continental shelf (Tesch, 2003). The northerly flowing Continental Shelf Current (Fig. 7; Reid *et al*., 1997; Malcolm, Godfrey & Youngson, 2010) and wind-driven local coastal currents (e.g. Fernand *et al*., 2006), thus, may play an important role influencing the final stage of landfall of glass eel. The combination of exposure to the leading edge of the North Atlantic Drift and Continental Shelf Current (Holliday & Reid, 2001) and the additional effect of south-westerly prevailing winds, particularly during the period from September to November when glass eels are likely to be appearing to the west of the U.K. (Tesch, 2003), means that the west of the British Isles and very particularly western Scotland is likely to be a region of first landfall for a large proportion of the oceanic migrating eel population in most years.

There is evidence that glass eels use both active swimming as well as tidal streams to aid migration into estuaries (McCleave & Kleckner, 1982). Thus, it is possible that glass eels exert some control over their ultimate freshwater destination. If active dispersal of glass eels into estuaries following landfall were, at least partially, density dependent, then during a period of low glass eel numbers, fewer may need to disperse actively beyond the first suitable coastal and freshwater habitats.

An alternative but related explanation is that secondary dispersal by glass eels following landfall could be mediated through body condition. Edeline *et al*. (2006) have shown that some settlement decisions by glass eels are body state dependent, with individuals in good condition more likely to choose to ascend into fresh water, whilst those in poor condition show a greater inclination to settle in brackish or saline water. There is also evidence that glass eels in some parts of Europe have decreased in both length and weight since the onset of the present recruitment decline, perhaps due to poorer feeding conditions in the Atlantic (Desaunay & Guerault, 1997; Knights, 2003; Bonhommeau *et al*., 2008). Thus, if there is a tendency for generally declining body size amongst settling larvae, and if this is linked to an increased tendency for settlement at the earliest opportunity, this might in part explain sustained recruitment in western Scotland.

This type of explanation could also explain the reported stability of freshwater resident populations elsewhere (e.g. in western England and Wales (Bark *et al*., 2007); in north-west France (Acou *et al*., 2011); in north-west Spain (Lobón-Cerviá & Iglesias, 2008); and in parts of western Ireland (ICES, 2010).

There is only a very limited understanding of the dynamics of settlement of glass eels as they enter fresh waters, hampering a complete understanding of the mechanisms that may be affecting recruitment to the freshwater populations. However, we argue here that the stability of the eel populations in Loch Lomond and the Allt Coire nan Con, and possibly elsewhere in western Scotland, which contrast distinctly with most of the rest of Europe, is most likely a consequence of regional-scale processes specifically related to the proximity of suitable freshwater recruitment sites in this area to the prevailing North Atlantic currents and winds.

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