REVIEWS

A review of glass eel migratory behaviour, sampling techniques and abundance estimates in estuaries: implications for assessing recruitment, local production and exploitation

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Abstract Recruitment of the three northern hemisphere eel species (European eel *Anguilla anguilla*, American eel *Anguilla rostrata* and Japanese eel *Anguilla japonica*) has reduced significantly over the past thirty-five years. The stock of the European eel is described as being outside safe biological limits, with urgent action required by European Union Member States to assist recovery of the panmictic stock. Stock recruitment models and estimates of silver eel output from a river catchment are strongly influenced by the degree of certainty in estimating key population parameters of each life history stage. Therefore, management decisions aimed at enhancing eel populations rely on sound scientific evidence, based upon a fundamental understanding of the complex anguillid eel life cycle. This review paper focuses on the estuarine entry phase of the eel life cycle and synthesises the current scientific knowledge with regard to glass eel migratory behaviour, sampling methods and abundance estimates within estuaries. Although the behavioural and environmental processes modulating glass eel migration patterns are reasonably well understood, site specific factors play a significant role in determining fine scale distribution patterns at an individual estuary level. Given the large resource commitment required to adequately sample this key life history stage, behavioural studies of migration patterns on a local scale are crucially important to aid the design of robust sampling programmes aimed at quantifying seasonal abundance and annual recruitment.

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Introduction

Recruitment of the three northern hemisphere eel species (European eel *Anguilla anguilla*, American eel *Anguilla rostrata* and Japanese eel *Anguilla japonica*)

has reduced significantly since the 1970s and 1980s. The stock of the European eel *A. anguilla* has recently and repeatedly been described as being outside safe biological limits, with urgent action required by European Union (EU) Member States to assist recovery of the stock to sustainable levels (ICES 1999 and thereafter). European glass eel recruitment (measured Europe-wide) has declined to <5 % of the average level from 1969 to 1980 (ICES 2012). A recent study on recruitment trends of juvenile eels in tributaries of the River Thames, UK has indicated declines of over 99 % (Gollock et al. 2011). Similarly, fisheries-based indices of glass eel recruitment to the Bristol Channel and Severn Estuary system (the largest and most significant contributor to the UK glass eel fishery) suggest recruitment has declined by approximately 70 % from its recent peak in the late 1970s (Bark et al. 2007). Furthermore, yellow eel populations resident in the Bristol Channel at Bridgwater Bay in 2009 had declined to only 1 % of that in 1980, based on time series data of eel impingement at power station intake screens (Henderson et al. 2012). The American eel *A. rostrata* has exhibited similar declines to that of *A. anguilla* since the 1980s (Castonguay et al. 1994; Haro et al. 2000; Richkus and Whalen 2000; Wirth and Bernatchez 2003; MacGregor et al. 2008). For example, *A. rostrata* recruitment to Ontario waters in east-central Canada has declined by 97 % since the early 1980s (Mathers and Pratt 2011). Concurrent declines in recruitment have also been observed in the Japanese eel *A. japonica* (Knights 2003) over a similar timescale. Anguillid eel populations in the southern hemisphere are also under threat, with Doole (2005) and Jellyman (2007) describing recruitment declines of up to 75 % in the New Zealand longfin eel (*Anguilla dieffenbachii*) since significant levels of commercial fishing began in the 1970s.

There are a number of anthropogenic impacts potentially affecting the recruitment level and survival of anguillid eels, with major impacts common for those species studied including commercial exploitation, habitat loss, dam and weir construction, hydropower, pumping stations and surface water abstractions (Richkus and Whalen 2000; Beaulaton and Briand 2007; Jellyman 2007; Defra 2010a; ICES 2012). Furthermore, the catadromous life cycle and panmictic reproductive life history trait of these species means that early ontogeny, larval migration and marine survival is heavily influenced by oceanic and climatic factors that are beyond the control of individual countries or states (Wirth and Bernatchez 2003, Als et al. 2011, Gagnaire et al. 2012, Côté et al. 2013).

One of the anthropogenic pressures affecting eel stocks in many EU Member States is commercial exploitation, including those fishing activities directed at the glass eel life stage (Beaulaton and Briand 2007; Bru et al. 2009; Defra 2010a; Briand et al. 2012). As a result of the European-wide decline in glass eel recruitment, the value of glass eels has increased considerably, multiplying a hundred-fold since the 1970s (Briand et al. 2008). This has coincided with a shift in export demand towards Japan and China (Briand et al. 2012), although this trade has been effectively banned since 2009 when European eel listing on Appendix II of the Convention on International Trade in Endangered Species (CITES) came into effect (CITES 2007). The majority of European glass eel fishing effort (87 % of European glass eel fisheries) is focussed in the estuaries draining into the Bay of Biscay (Beaulaton and Briand 2007). Here, in some estuaries, large numbers of 'civelliers', or boats utilising push nets, exert intensive fishing pressure on glass eels migrating upstream on the flooding tide. In the UK, the glass eel fishery is less intensive (restricted to a dip net fishery focussed mainly on the rivers draining into the Bristol Channel); however, the practice has recently become the focus of some concern with regard to the level of exploitation of the total yearly recruitment to the Severn River Basin District (RBD) and the resultant potential impact on silver eel production (Defra 2010b). Quantifying glass eel recruitment and commercial exploitation within individual estuaries is, therefore, important to inform future sustainable management practices.

This review collates and synthesises the current scientific knowledge relating to glass eel migratory behaviour and addresses considerations for assessing recruitment and exploitation in large estuaries. Throughout the text, the term 'glass eel' refers to young, unpigmented eel, recruiting from the sea into continental waters; 'yellow eel' refers to the life-stage resident in continental waters; 'silver eel' refers to the seaward migratory phase following the yellow eel phase (ICES 2012). While much of the text is focussed on *A. Anguilla*, where specified, knowledge is also drawn from research on other anguillid species worldwide.

Stock assessment of European eels

In response to the decline in European eel stocks, the EU adopted Council Regulation No 1100/2007/EC establishing measures for the recovery of the stock of European eel (EC 2007). This regulation requires Member States to develop Eel Management Plans (EMPs), with the objective of "reducing anthropogenic mortalities so as to permit with high probability the escapement to the sea of at least 40 % of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock".

The assessment framework is, therefore, designed around this management objective, and each Member State must provide estimates of the following stock indicators (ICES 2012):

$B_{current}$	The biomass of the escapement in the assessment year
B_{best}	The best achievable escapement under present conditions
B_0	The escapement under conditions of high recruitment and no anthropogenic impacts (the management target is 40 % of B_0)
$\sum A$	The sum of mortalities (over the whole life span) due to various anthropogenic impacts

From an England and Wales perspective, B_{best} was first estimated at the Water Framework Directive (WFD) RBD scale for selected "eel index" rivers using the Scenario-based Model of Eel Production II (SMEP II), which was validated as part of the EU "Pilot projects to estimate potential and actual escapement of silver eel" (POSE) (Walker et al. 2013). Other methods used to estimate production were hydroacoustics and mark-recapture studies on silver eel populations (Bilotta et al. 2011). The potential production of eel under present conditions in these eel index rivers was expressed in terms of silver eel biomass produced per unit wetted area, i.e. kg ha^{-1}. This production rate, or the mean value where > 1 river was assessed, was then applied to the wetted area of the entire RBD. As for the SMEP II model, hydroacoustics and mark-recapture estimates were all based on the freshwater parts of the river basins, therefore they did not take account of the potential effects of any glass eel fisheries in estuaries. Where such fisheries occurred, the reported catch was converted to a silver eel equivalent that was added to the modelled freshwater production to derive B_{best} for the RBD as a whole, reported as an annual biomass in kg. One kg of glass eels was considered equivalent to approximately 93.8 kg of silver eels, based on an instantaneous mortality of 0.14 year^{-1} (Dekker 2000) and a 50:50 sex ratio, with males maturing at 12 years (0.9 kg) and females maturing at 18 years (0.57 kg) (Aprahamian 1988, Defra 2012). B_0 was estimated using the same approach as that used to estimate B_{best}, using data collected in the early 1980s.

$B_{current}$ was estimated as 'B_{best} minus the losses due to anthropogenic impacts'. These losses were expressed in terms of biomass of silver eel equivalents and were calculated for the following anthropogenic activities: commercial fisheries; tidal flaps/gates; pumping stations; surface water abstractions and hydropower (Defra 2012). The estimates of B_0, $B_{current}$ and B_{best} rely heavily on the extrapolation of data from small study areas to the RBD as a whole, with the inherent possibility of bias. Furthermore, to derive an estimate of current production and anthropogenic mortality for the RBD from the available data a number of assumptions have been required; these have tended to be precautionary in nature (i.e. likely to underestimate current production and overestimate current anthropogenic mortality).

The fourth stock indicator is the sum of all anthropogenic mortalities ($\sum A$), which is calculated as '$-\ln (B_{current}/B_{best})$'. This stock indicator was first proposed by ICES Study Groups (ICES 2011a) and further developed by the EIFAAC/ICES Working Group on Eel (WGEEL) (ICES 2011b). The mortality rate target (A) was proposed as an additional management target because it is a measure that will respond more quickly to management measures than silver eel escapement biomass (which, depending on the eel stage affected in the UK, will take up to an eel maturation time of ~ 12 years for males and ~ 16 years for females (Aprahamian 1988) to become apparent). The rate for $\sum A$ was derived from the biomass target (40 %) such that the sum of all anthropogenic impacts, summed over the entire continental lifespan, should not exceed a rate of 0.92. Note, however, that $\sum A$ is calculated from values of silver eel equivalents, and therefore does not require a measure of exploitation rate for the glass eel fishery *per se*. This will be discussed in more detail later in this review.

Glass eel migratory behaviour and influence of environmental variables

The life cycle of the European eel has been extensively documented in previous literature and has not, therefore, been described in detail within the current review. Rather, the focus of the current work has been on the life stage related to estuarine entry and upstream passage into freshwater rearing habitats.

Anguilla anguilla spawn in the Sargasso Sea, after which the eel larvae (leptocephali) are passively and/or actively transported by marine currents towards the continental shelf of the Atlantic coast of Europe and North Africa (Tesch 1980). Upon nearing coastal regions, the willow leaf-shaped, translucent leptocephali metamorphose into glass eels and colonise coastal, estuarine and freshwater habitats (van Ginneken and Maes 2005).

Glass eels enter estuaries all year round, with migration peaks depending on latitude and also the variability of oceanic factors. For example, in southwest Spain, Arribas et al. (2012) found that highest densities occurred between late autumn and spring, with two migration peaks observed. Short term (monthly) changes in glass eel density were reported to be partially driven by local environmental variables, such as turbidity, rainfall and temperature; whereas long term (inter-annual) changes were also associated with factors relating to recruitment success, such as the North Atlantic Oscillation (NAO) index and primary production at the spawning area (Arribas et al. 2012). In contrast to the more southerly populations, peak glass eel migration in the UK is later, typically occurring from February to May (Defra 2010a).

Selective tidal stream transport

Due to their anguillid body shape and small size, glass eels have relatively limited locomotory capabilities, with mean critical swimming speeds of 11.7–13.3 cms^{-1} being quoted for *A. rostrata* glass eels over a temperature range of 14–24.5 °C (Wuenschel and Able 2008). Furthermore, it has been quoted that glass eels of both *A. rostrata* and *A. anguilla* cannot swim "for very long" against currents exceeding 30 cms^{-1} (Adam et al. 2008). The ability of glass eels to actively migrate upstream throughout an estuary system against the river flow is, therefore, limited.

Passive upstream migration using 'Selective Tidal Stream Transport' (STST) has been described by various authors as a mechanism by which fish with low swimming capabilities can progress upstream throughout an estuary system utilising tidal currents (McCleave and Kleckner 1982; Gascuel 1986; Beaulaton and Castelnaud 2005). Essentially, if a fish remains on or near the bottom during ebb tides and moves into the water column on flood tides, it will effect a nett migration towards freshwater with relatively little expenditure of energy. Using this strategy, juvenile fish have been shown to save up to 90 % of the energy that would otherwise be expended swimming the same distance (Weihs 1978).

STST is widely accepted to be the main mechanism utilised by glass eels of all studied species in upstream migration through estuaries towards freshwater (Deelder 1958; Creutzberg 1958, 1959; Jellyman 1979; McCleave and Kleckner 1982; Sheldon and McCleave 1985; Gascuel 1986; Wippelhauser and McCleave 1987; de Casamajor et al. 2000a; Sughea et al. 2001; Dou and Tsukamoto 2003; Bru et al. 2009; Trancart et al. 2012). Orientation towards the bottom during ebb tides has also been demonstrated experimentally, whereby glass eels buried into the substratum in order to maintain a stationary position (Trancart et al. 2012). The vertical migrations associated with STST are hypothesised to be under the control of endogenous rhythms (biological clock), rather than exogenous cues such as odour, turbulence or electrical fields, with the result that glass eels often ascend from the bottom when the tide is still ebbing (Wippelhauser and McCleave 1987). However, the mechanisms of this behaviour are unclear, given that tidal strength and duration varies both spatially and temporally. Indeed, it seems plausible to assume that glass eels, at least in the later stages of development, must also utilise exogenous cues related to river flow and tidal strength in order to control the timing and duration of vertical migrations.

This mode of transport, therefore, has consequences for the vertical and horizontal distribution of glass eels both throughout and between tidal cycles, and hence their susceptibility to sampling gears. For example, McCleave and Kleckner (1982) found that *A. rostrata* glass eel catches were always much greater in mid-channel samples during flood than during ebb tides, and that glass eels were captured throughout the water column on flood tides but only near the bottom

during ebb tides. Furthermore, in stratified estuaries, glass eels stay in or below the halocline on the flood tide. However, Sheldon and McCleave (1985) also demonstrated that, at all stages of the tide, glass eel density at the surface was greater at more landward stations than at more seaward stations, and greater near the shore than in mid-channel.

Sheldon and McCleave (1985) found that *A. rostrata* glass eels progressively migrate upstream just behind the tidal front. Gascuel (1986) also describes a natural 'trapping' of *A. anguilla* glass eels during the flood tide in an area the location of which is determined by the strengths of the freshwater flow and flood tide. As this flux of glass eels moves upstream, their density increases in a lower volume of water (Gascuel 1986).

Although STST can explain the general mechanism by which glass eels effect a nett upstream migration through estuaries, synchronisation of tidal stream transport is weak under constant flow conditions and therefore glass eels might necessitate several environmental cues related with flood tides to remain synchronised (Bolliet et al. 2007). Examination of the cross correlations between the catches of the "pibalour" fishery downstream in the Gironde Estuary and the dip net fishery upstream revealed a migration speed of 3–4 km/day, indicating that, in the case of the Gironde Estuary, the distance covered was only 15–19 % of that which could have been covered with fully effective use of the tide (Beaulaton and Castelnaud 2005).

Active migration in upper estuaries

Although STST is the primary mechanism facilitating migratory passage through estuaries, where tidal effects become weaker in upper estuarine zones, a behavioural shift to active swimming is necessitated to effect further dispersion upstream. This was first described by Deelder (1958) as a progressive trend to migrate counter current towards freshwater. At the freshwater interface (Tesch 2003), or more certainly from the point where they accumulate (McCleave and Wippelhauser 1987), glass eels change their behavioural pattern (Creutzberg 1961) and actively migrate counter current. Such an active migration is revealed in the 'crawling' behaviour that glass eels display on trapping ladders (Tesch 2003; Legault 1988; McGovern and McCarthy 1992) and in their tendency to

school and to swim close to the shore, as described for *A. anguilla* (Vilter 1944; Tesch 2003), *A. australis* (short-finned eel) and *A. dieffenbachii* (Jellyman 1979).

Jellyman (1979) notes that for both *A. australis* and *A. dieffenbachii*, this 'second phase' of migration, when glass eels adopt a more active swimming approach, can often be the more convenient stage for capture, as the eels move in large shoals forced close to the shore by the ebb tide (Jellyman and Lambert 2003). Within riverine reaches of the Waikato River in New Zealand, movement can occur at any stage of the tide; however, glass eels become more concentrated adjacent to the banks during ebb tides and more dispersed during flood tides.

Water temperature is considered a major factor stimulating the onset of this active swimming behaviour, with critical temperatures of between 10 and 15 °C quoted for both *A. anguilla* (Gascuel 1986; Briand 2009) and *A. rostrata* (Overton and Rulifson 2009). In the UK, temperatures of 10–11 °C have been demonstrated as a critical threshold for pigmented elvers ascending weir or sluice barriers (White and Knights 1997). At a salinity of 10 ppt the transition from passive to active migration would take 50 days at 8 °C but will reduce to a little more than 2 weeks at 12 °C (Briand 2009). In the Vilaine, the duration of this period of active migration for *A. anguilla* was observed to be very short, generally lasting between three and 10 days (Briand 2009), after which the glass eels settle as elvers. However, this will be specific to the haline and thermal dynamics of the estuarine system, which will be influenced by estuary length, spatial complexity, tidal magnitude and freshwater inputs.

Figure 1 below provides a generalised summary of glass eel migration in upper estuaries, where they utilise a combination of STST and active swimming behaviours. During the flood tide, glass eels are spread throughout the water column and passively migrate upstream utilising the flood tide current. During the slack and early ebb tide, glass eels move to the margins and actively swim upstream for a short period until the current speed exceeds their sustained swimming capability. During the full ebb tide, glass eels move to the bottom and remain on or in the substrate in order to maintain their position in the estuary and avoid being carried back downstream by the ebb tide current and river flow (Deelder 1958; Creutzberg 1959;

Fig. 1 Generalised summary of glass eel migration in upper estuaries. Flood tide; glass eels spread throughout water column. Slack/early ebb tide; glass eels move to margins and actively swim upstream. Ebb tide; glass eels remain on or in the bottom substrate
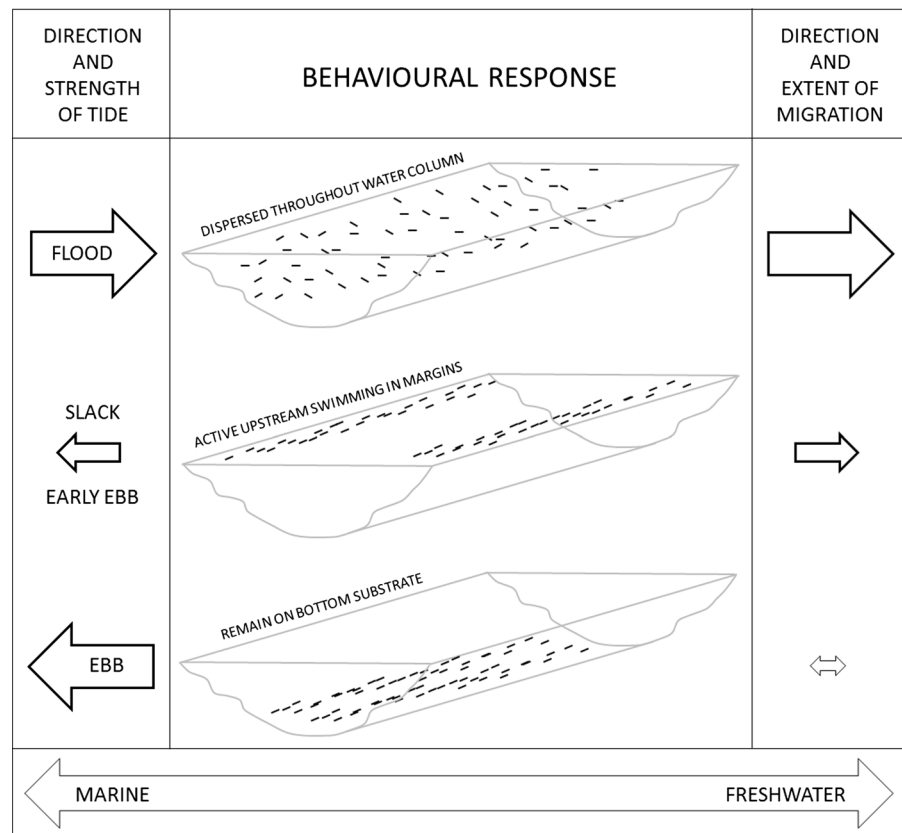
Jellyman 1979; McCleave and Kleckner 1982; Sheldon and McCleave 1985; Gascuel 1986; Wippelhauser and McCleave 1987; de Casamajor et al. 2000a; Sughea et al. 2001; Dou and Tsukamoto 2003; Bru et al. 2009; Trancart et al. 2012).

Influence of light intensity and turbidity

Glass eel behaviour is influenced by light levels (Fontaine 1950), with an increase in activity during the first hours of darkness (Bardonnet et al. 2003; Bureau Du Colombier et al. 2007), during which time they also distribute closer to the surface. This directly influences their catchability in turbid or dark conditions (Elie 1979; Jellyman 1979; Gandolfi et al. 1984; Gascuel 1987) compared to when in clear water during daylight (de Casamajor et al. 1999, 2000a). However, simulations using a behavioural model developed to model the impact of hydroclimatic conditions on glass eel behaviour and the speed of upstream migration within the Adour Estuary demonstrated that glass eels must migrate during the day as well as during the night

if the speed of upstream migration is to be explained (Prouzet et al. 2009; Adam et al. 2008). This was confirmed in the Gironde Estuary, with an estimate of 30 % of glass eels migrating during the day (Lambert et al. 2007).

Influence of lunar cycle and tidal amplitude

Various authors have demonstrated increased abundances in glass eel catches during the new moon phase, but not the full moon, despite the fact that the tidal amplitude during both periods is similar (reviewed by Adam et al. 2008). This could potentially be explained by the effect of the lunar cycle on light intensity, and hence glass eels remaining deeper in the water column during the full moon, resulting in reduced susceptibility to fishing gears. This effect of the lunar cycle and hence moonlight intensity is modulated by cloud cover and turbidity; therefore, one consequence is the fact that the lunar effect is not observed in highly turbid estuaries (Lafaille et al. 2007).

Although the majority of glass eels migrate on the flood tide at night, some do enter the water column during the ebb tide (Elie 1979; McCleave and Kleckner 1982; Sheldon and Mccleave 1985). In the Isle, a tributary located upstream in the Gironde Estuary, it was estimated that the number of glass eels present in the water column during ebb tides was 16 % of that during flood tides (Lambert et al. 2007). However, clearly these glass eels will not be able to progress upstream against the current and, indeed, are likely to be returned downstream by the ebb tide. Whether such behaviour results in eventual recruitment to freshwater, settlement within the estuary or elevated rates of natural mortality, is currently unknown.

Influence of river flow

River flow has been demonstrated to be an attracting cue that may play a positive role on the abundance of glass eels at fisheries (Crivelli et al. 2008; Arribas et al. 2012). However, high flows can have a countering effect on tidal flow in the 'upstream' direction thereby reducing the conveyor belt effect of STST. During high river flows, glass eels may congregate in slacker water close to the banks of the lower estuary, likely resulting in increased predation and exploitation risk. This 'backlog' of glass eels would be expected to move up the estuary using STST once river flows recede (Ben Abdallah 1991; de Casamajor et al. 2000b; Adam et al. 2008, Bru et al. 2009). Furthermore, higher river flows are typically accompanied by higher concentrations of suspended sediments and increased turbidity, resulting in a high density of eels spread throughout the water column and near the surface after flood events in estuaries with naturally low turbidity (Bru et al. 2009).

In addition to the rheotactic influence of river flow on upstream migration, olfactory cues associated with freshwater are also considered important in the modulation of glass eel migratory behaviour (Creutzberg 1961, Crnjar et al. 1992, Tosi and Sola 1993, Sola 1995, Briand et al. 2002, McCleave and Jellyman 2002, Tesch 2003, Edeline et al. 2009). Eels have a well developed sense of smell, with the olfactory rosette and nasal cavity in glass eels being similar to those exhibited by adults of other fish species (Tesch 2003). The smell of freshwater may act as both a behavioural 'cue' (e.g. triggering increased swimming activity during STST) and a directional 'clue' (e.g. facilitating orientation towards inland waters) (Edeline et al. 2009). Earthy odorants, such as geosmin, associated with inland waters are thought to be particularly important as attractants in orientation towards freshwater (Tosi and Sola 1993, Sola 1995). In addition, glass eels are also attracted by the odour of adult conspecifics, which may facilitate orientation towards optimal habitat (Briand et al. 2002, Tesch 2003, Edeline et al. 2009).

Influence of temperature

Low temperatures (less than 6 °C) have been demonstrated to reduce glass eel activity (Deelder 1958; Elie 1979; Cantrelle 1981; Lecomte-Finiger and Razouls 1981; Gascuel 1986; Désaunay et al. 1987; Elie and Rochard 1994), and as they cease their vertical migration they presumably become much less susceptible to fishing gears.

In general, there is a positive correlation between temperature and upstream migration speed. In the Loire estuary, increasing temperatures are negatively correlated with the catch of marine fishermen and positively correlated with the catch of fluvial fishermen (Ben Abdallah 1991). However, the catchability of glass eels is reduced at temperatures greater than 10 °C (Laffaille et al. 2007) or 11 °C (Désaunay et al. 1987). This may be explained by increased developmental rates and a resultant rapid shift to active migration and 'early' settlement of elvers as temperatures increase (Briand 2009).

Estuarine settlement versus upstream migration

Not all glass eels arriving in an estuary will necessarily choose to migrate upstream into freshwater. Using evidence from the carbon signature in stable isotope analysis, Bardonnet and Riera (2005) suggested that estuaries may function as important feeding/rearing habitats, in addition to their function as a migratory corridor. Furthermore, extensive and ongoing research into otolith microchemistry (Sr/Ca ratios) has demonstrated that some glass eels may settle in the estuary indefinitely (Tzeng et al. 1997; Jessop et al. 2008; Bureau Du Colombier et al. 2011), while others may display a transient behaviour moving back and forth between freshwater and marine systems during the rearing process (Tsukamoto and Takaomi 2001).

Internal drivers, such as body condition and endocrine control, are suggested to play an important role in the propensity of some glass eels to settle within estuaries rather than continue to migrate upstream to freshwater habitats (Edeline et al. 2005, 2006, 2009). Under experimental conditions, glass eels with a lower body condition have been shown to prefer saltwater over freshwater, with the authors suggesting that in the wild, this condition-dependent change in salinity preference in glass eels induces an early settlement in marine or estuarine habitats (Edeline et al. 2006). This behavioural shift is hypothesised to be adaptive in limiting the probability of death due to exhaustion through river-orientated migratory behaviour. Hence, settlement within an estuary or continued migration into freshwater may be determined by an individual's energy content on estuarine arrival.

Glass eel dispersal is also influenced by endocrine control, with thyroid hormones being demonstrated to stimulate migratory behaviour (Edeline et al. 2005). Thyroid hormones are thus suggested to play a key role in the regulation of physiological and behavioural adaptations leading to the upstream migration and colonisation of freshwater habitats by glass eels (Edeline et al. 2009). In addition, cortisol (a stress hormone) production promotes gill and intestine Na^+/K^+—ATPase activity; an adaptation for salt water residency (Wilson et al. 2004). It is hypothesised that an increase in cortisol (in synergy with growth hormones) mediated by lower body condition on estuarine arrival is linked to decreased production of thyroid hormones, resulting in a shift from upstream migration to estuarine settlement (Edeline et al. 2009).

The onset of exogenous feeding in *A. anguilla* has been confirmed in some leptocephali before they leave the Saragasso Sea (Riemann et al. 2010). This pelagic phase of ontogeny facilitates both transatlantic transport and the accumulation of endogenous energy reserves which are then relied upon when the larvae reach the Eastern Atlantic shelf and undergo morphogenesis. It is during and beyond this ontogenetic threshold that glass eels rely exclusively on endogenous energy reserves whilst migrating across the shelf (Boetius and Boetius 1989). Despite reports of exogenous feeding behaviour resuming on arrival within estuaries (Désaunay and Guérault 1997), feeding has been shown to occur in only some individuals after capture in net fisheries in the UK (P. Wood, UK Glass Eels, pers. comm) and this may provide an advantage

in the ability of some individuals to complete their upstream migration into freshwater (Bureau Du Colombier et al. 2008).

The condition factor of recruiting glass eels has previously been linked to the timing of estuarine arrival, with early season recruits generally having a higher condition factor than those arriving later in the season (Bureau Du Colombier et al. 2007, 2011). Other researchers have reported the abundance and length of glass eels entering European estuaries in the autumn being greater that those arriving in the summer, hypothesising that the transatlantic migration of these later recruits from the Sargasso Sea is undertaken during spring and summer, when oceanic productivity is likely to be maximised (Désaunay and Guérault 1997).

While it has been hypothesised that the sharp decline in glass eel abundances observed Europe-wide since the 1980s could partly be explained by changes in oceanic plankton abundance, affecting a decrease in glass eel energy stores (Bureau Du Colombier et al. 2008), the understanding and quantification of such effects are likely to be further complicated by inter-annual variations in oceanic currents and transatlantic transport times (van Ginneken and Maes 2005).

With respect to the ecological implications of settlement strategy, glass eels that settle in estuaries may be afforded increased growth prospects. This may be manifest through the relatively higher productivity and carrying capacity of estuarine habitats which contrast with the inherent increase in density dependence effects within freshwater systems. Indeed, using otolith microchemistry, Jessop et al. (2002) demonstrated that juvenile *A. rostrata* that remained in the estuary for 1 year or more before entering the river contributed to silver eel production to a significantly greater extent than did elvers that entered freshwater during their year of arrival. It was hypothesised that this could be due to the relatively high mortality rate of glass eels in the river compared with those that remained in the estuary during the first year or more of life after recruitment (Jessop et al. 2002). Other researchers, however, have suggested that estuarine and marine habitats are colonised by yellow eels rather than glass eels, with precocious settlement of glass eels in estuaries being prevented by competition with estuarine residents and downstream nomads (Daverat and Tomas 2006).

A tendency for some eels to settle in estuarine environments (either naturally or as a result of barriers

to upstream migration) may also have implications for upstream population dynamics and silver eel escapement biomass due to the role of environmental factors in sex determination of anguillid species. In particular, males are generally observed to dominate in high density environments, often associated with estuarine or lower river reaches, whereas females tend to become increasingly dominant with increasing distance from the sea (Parsons et al. 1977, Davey and Jellyman 2005, Lafaille et al. 2006, Adam et al. 2008). It is suggested that a "grow quickly, mature early" life history strategy exhibited by male eels under conditions of high density may increase an individual's chances of survival during periods of increased intraspecific competition (Lafaille et al. 2006).

Assessing glass eel recruitment to estuaries

It is worth highlighting at the outset that, currently, abundance estimates of glass eels are restricted to riverine or upper sections of small or medium sized estuaries (Tzeng 1984; Jessop 2000; Briand et al. 2006; Adam et al. 2008; Bru et al. 2009), where glass eel sampling is relatively straightforward, though by no means easy. In contrast, quantification of glass eel fluxes have not been assessed at the estuary mouth or in large open environments such as the Bristol Channel in the UK, with limiting factors relating to the "*significant, even colossal, resources required*" rather than to methodological issues (Adam et al. 2008).

Sampling glass eels in estuaries

The efficacy of any sampling gear will depend on the volume of water it can filter relative to the total circulating volume, and its capacity to function at different depths and under different hydrodynamic conditions (Adam et al. 2008). Furthermore, glass eel catchability in some estuaries is highly dependent on environmental variables, being maximal when the water is turbid and upstream migration is slow, i.e. low or medium tide coefficient combined with a medium river flow (Bru et al. 2009). With this in mind, several methods are commonly used for capturing glass eels within estuary systems, and these are highlighted below.

A relatively straightforward and reliable approach to sampling glass eels (or elvers) migrating upstream from the estuary into fresh waters is to install and monitor an elver trap at a suitable obstacle to migration where the glass eels will congregate, such as a tidal barrier. Counts of catch per unit time can provide seasonal abundance estimates (EA 2011). However, care must be taken to ensure that all eels are passing through the trap or, if not, that the proportion bypassing the trap is known (Jessop 2000). This method has been used to estimate the exploitation rates of *A. rostrata* by a commercial dip net fishery by calculating the number of glass eels captured by dip nets as a proportion of the overall riverine recruitment estimated via elver traps (Jessop 2000). However, this approach would not take account of the natural mortality and settlement that are likely to occur between the location of the dip net fishery and the elver traps upstream.

Other passive sampling techniques, such as the use of artificial habitat collectors (Silberschneider et al. 2001), are useful for providing information on relative abundance and spatial distribution of glass eels throughout estuary systems; however, quantitative overall abundance estimates cannot be provided with these approaches.

Commercial glass eel fisheries tend to utilise two main sampling techniques; nets deployed from a boat (either push nets or pelagic trawls) and handheld dip nets deployed from the shore (Jessop 2000; Jellyman and Lambert 2003; Bru et al. 2009; Briand et al. 2012). The only approach currently legal in the UK is to use handheld dip nets from the shore (Defra 2010a). Although relatively limited in terms of the spatial extent of surveying, handheld dip nets can prove highly effective in capturing glass eels due to the behavioural and hydrodynamic factors previously discussed, whereby eels are often concentrated in particular locations and therefore susceptible to exploitation from the shore. As a result, commercial fishermen tend to concentrate fishing effort during times and in locations where catch probabilities are optimal. In contrast, commercial fishing from boats (common on the French Atlantic coast) enables fishermen to exploit most of the estuary using nets generally ranging in size from 1.2–1.5 m^2, but up to 7 m^2 in the Gironde Estuary (Gascuel et al. 1995). Boat fishing is usually conducted during the flood tide,

when glass eels are distributed throughout the water column and are more susceptible to capture.

Abundance estimates of glass eels in estuaries

A glass eel flux can be described as a number of glass eels migrating into or upstream in an estuary during a given time interval, e.g. a single incoming tide, a day or a season (Adam et al. 2008). In order to accurately estimate glass eel recruitment into an estuary, therefore, it is necessary to monitor the ingress of eel numbers throughout the course of the year by utilising a standardised sampling methodology, and subsequently extrapolate the resulting data into an overall abundance estimate for the entire estuary over the full season.

For a successful quantitative assessment of the abundance of glass eels entering an estuary, the time and area (e.g. the wetted cross section) must be clearly defined, which relates to the volume of water. The complex spatial heterogeneity in glass eel distribution relating to environmental variables (described above) is one of the main confounding factors in assessing overall estuarine recruitment and must also, therefore, be considered within the sampling design (Adam et al. 2008). For example, sampling must be conducted over the whole water column (or at least surface and mid-water) and across the whole width of the channel (or at least right bank, middle and left bank). Furthermore, the sampling area/cross section should ideally be (1) under the influence of the dynamic tide to avoid merging of various glass eel fluxes entering the estuary in successive tides, (2) linear and, if possible, canalised to avoid flux aggregation, and (3) non-stratified (haline or thermal) to avoid trapping of glass eels below the halocline/thermocline (Adam et al. 2008). Importantly, once a sampling methodology has been designed and calibrated, this protocol should be strictly adhered to throughout the course of the monitoring period (Adam et al. 2008) to ensure the resulting data are comparable. However, it may be necessary to vary the survey design from year to year until the optimum design is achieved. This iterative survey design will compromise between-year comparisons, but is almost inevitable when commissioning new work in such dynamic and challenging environments.

Jessop (2000) estimated the maximum exploitation rate of *A. rostrata* glass eels by a dip net fishery in the

East River, Nova Scotia to range from 30.8 to 51.8 %. The total glass eel run was estimated by combining commercial dip net fishery data with daily counts of glass eels captured in eel traps at the first migration barrier. Exploitation rates were then calculated as the daily, seasonal or annual number of eels captured by the fishery as a proportion of the total glass eel run (Jessop 2000). Similarly, exploitation rates of *A. japonica* ranging from 44.1 to 75.4 % were demonstrated for a hand trawl fishery in a Taiwanese river (Tzeng 1984). Although seemingly quite high, Jessop (2000) suggests that exploitation rates by a dip net fishery of 30–50 % may actually have little effect on yellow or silver eel production where the mortality rate of elvers is naturally high.

Bru et al. (2009) studied recruitment at a single sampling station in the Adour Estuary from 1998 to 2005. The sampling station was chosen to maximise glass eel catch efficiency and minimise the effects of hydrodynamic and environmental variables. The estuary at the sampling station was approximately 300 m wide, rectilinear with no hydrodynamic turbulences and un-stratified. Sampling was conducted using push nets from a boat, cruising 5 min seaward transects against the flood tide with nets set at depths of 1 m and 4 m. The right bank, middle and left bank were all sampled within 30 min and repeated to provide 8 replicates per tide. Complex statistical models were used, based on the 6 year dataset, to extrapolate the catch to total glass eel abundance per night/day/season and to estimate the commercial exploitation rate. However, even with such a large dataset, collected in a standard format within a relatively small and strictly defined sampling station, these data displayed a high degree of variation in abundance estimates. This highlights the importance of the heterogeneous nature of glass eel distribution within estuaries and the confounding influences of the many hydrodynamic, environmental and seasonal factors influencing their abundance.

A simpler approach was adopted in the Minho Estuary on the Portugal-Spain border (Adam et al. 2008). The sampling station was approximately 7.5 km from the estuary mouth, where the estuary was 620 m wide, 3.7 m deep, with a tidal range of 0.6 m. The right bank, middle and left bank were sampled simultaneously using three fixed nets, 10 m wide and covering the entire water column. Samples were collected on the incoming tide during nights of

the new moon phase. The number of glass eels migrating through the whole sampling station during the entire flood tide was estimated from the sampled catch densities extrapolated to the total circulating volume.

Both approaches make assumptions about the distribution of glass eels outside the sampled areas and on nights when sampling did not take place. To validate such assumptions initial extensive sampling programmes would be required. Although reference to other studies can be useful, the individual nature of each estuary environment means that there is no substitute for local data.

The 'Glass Eel Model to Assess Compliance' (GEMAC), was developed by Briand et al. (2006) to investigate the effect of glass eel fisheries and intake pumping on the number of settled glass eels per area within a specified estuary. One of the main features of the model is that it can be applied to estimate the recruitment of glass eels at the mouth of an estuary, either as a monthly recruitment index according to the latitude, or a daily recruitment index if parameters such as flow and temperature are known. It has been applied to the Gironde Estuary which is approximately 8 km wide. However, application of this model to larger estuaries, such as the Bristol Channel in the UK (~20 km wide) would need to be tested.

Sampling glass eels in large estuaries and coastal waters

As discussed above, attempts by various authors to estimate glass eel abundance have mainly been limited to the upper estuary or more riverine sections, where a relatively discrete sampling station can be selected that is subject to minimal environmental and hydrodynamic confounding factors. In contrast, estimating glass eel abundance at the estuary mouth or indeed coastal waters (such as the large and exposed area of the Bristol Channel, UK) presents significant challenges, not least in adequately sampling the area/volume and extrapolating the resultant catch data.

For example, the Bristol Channel is the largest estuarine system in the UK, with an area of 4800 km^2. It experiences the third highest tidal range in the world, exceeding 14.5 m at Avonmouth (Henderson et al. 2012). At Bridgwater, the Bristol Channel is approximately 20 km wide, with a very fast tidal flow and high turbidity (Bark et al. 2007). The strong tidal

currents in the Bristol Channel make sampling using traditional techniques problematic. For example, previous attempts to capture yellow eels using beam trawls have been unsuccessful due to the sediment depth and instability (Henderson et al. 2012). Sampling small fish such as glass eels within the Bristol Channel would pose additional logistical and methodological problems. For example, the high loadings of suspended silt may limit the use of fine mesh ichthyoplankton push or trawl nets that would be required to sample these small life stages in sub tidal habitats, though there may be greater potential to use fine meshed nets in intertidal zones with reduced velocities. Similar problems would likely be encountered with fine meshed fixed sampling gear, such as stow nets. Trials of various sampling gears and methodologies would be required to assess the options for surveying glass eels in such a challenging environment.

Regardless of the sampling gear used, one of the main perceived problems with sampling such a large area would be the resource requirements to conduct a statistically robust sampling design. Dutil et al. (2009) investigated the abundance of *A. rostrata* glass eels in the Gulf of St Lawrence on the Atlantic coast of Canada using long term (1948–1998) ichthyoplankton trawl data supplied by the Department of Fisheries and Oceans. Out of a total of 9,999 samples from 58 surveys in which all fish larvae were identified, a total of only 85 glass eels were recorded from 53 samples. Most glass eels were captured at the surface using horizontal surface tows.

Long-term data demonstrating the decline of *A. anguilla* glass eel recruitment to the Skagerrak-Kattegat area of Sweden has been gathered as part of the ICES International Bottom Trawl Surveys (previously referred to as the International Young Fish Surveys), using a modified Methot-Isaac-Kidd midwater trawl (Hagstrom and Wickstrom 1990; Durif et al. 2011; Dekker 2012). However, the number of glass eels captured since 1990 is very low, with no glass eels being recorded in recent years (Dekker 2012). These data highlight the highly under-dispersed nature of glass eel fluxes in open water and the resultant low probability of capture. The ideal survey design would, therefore, necessitate a large number of samples distributed both horizontally and vertically across the sample area. The recruitment season extends over several months and there is no reason

to assume that recruitment is evenly dispersed across time, therefore, surveys would be required throughout the season. Furthermore, inter-annual variability in glass eel recruitment means that seasonal datasets collected over a number of years would be required to quantify mean annual recruitment.

Sampling glass eel entrainment into power station cooling water intakes in estuarine or coastal environments can also provide useful data on seasonal recruitment patterns; however long-term datasets of eel entrainment at power stations generally relate to impingement of adult eels on in-works screens, which can be sampled relatively easily (e.g. Henderson et al. 2012). In contrast, a large proportion of glass eels are likely to be entrained through the in-works screens, which tend to have a larger mesh size than that required to exclude these smaller life stages and glass eel are, therefore, not fully accounted for within impingement samples. This may be overcome by sampling with a fine meshed net within the cooling water intake before the in-works screens (Dekker 2012). However, although a relatively robust estimate of the seasonality of recruitment and long-term trends in relative abundance could be established using this method, extrapolating these limited data collected at one location to estimate total recruitment to the estuary would be problematic.

Using glass eel recruitment data in assessing local production and exploitation

The derivation of seasonal abundance estimates of glass eel recruitment would facilitate direct calculation of the level of glass eel commercial fishing mortality, along with other anthropogenic impacts occurring at the glass eel stage, such as entrainment into estuarine power station cooling water abstractions. However, considering the often discrete nature of glass eel sampling in estuaries, some assumptions about glass eel mortality during estuarine residence and the pattern of migration would have to be provided.

Direct estimates of mortality at the glass eel stage are not currently used in England and Wales Eel Management Plans, with the glass eel catch being converted to a silver eel equivalent. However, there remains considerable uncertainty in various aspects of the assessment procedure with regard to estimating the

biomass of silver eel equivalents, particularly at a local level, and data on glass eel recruitment could be applied in several different ways.

One way, applicable to the England and Wales context, but also likely to be applicable Europe-wide, would be to improve the confidence associated with the extrapolation of glass eel numbers to silver eel equivalents, which at present does not take account of local conditions, e.g. the productive potential of habitats influencing growth rates, density-dependent factors and other impacts. For example, where growth rates are relatively slow it will take more years for eels to reach the length required to become a silver eel (Vollestad 1992) and, because natural mortality may occur throughout the life of the eel, the probability that a slow growing individual will reach that critical length may be lower than that for an eel in an environment that allows faster growth. A further current assumption is that density dependent natural mortality is a significant impact on glass eel recruits within the estuary and lower reaches of rivers (Bark et al. 2009); however, it is difficult to prove this scientifically. The natural mortality of small eels is likely to be high compared to older eels due to the fact that more animals can prey on the smaller life stages and they occur in higher densities. However, the natural mortality of these early life stages is also the least well understood because of the significant challenges in repeatedly catching small eels in such a way as to provide robust quantitative estimates of their abundance. An estimate of the number of recruits in any year, along with estimates of yellow eel production from that age cohort in subsequent years, would provide indirect but locally relevant estimates of age- or size-specific natural mortality rates in young eels, which can be used to improve the "glass eel to silver eel" conversion rate, and hence the contribution of the glass eel fishery to the sum of mortalities due to all anthropogenic impacts ($\sum$A), as required by the EU.

From a UK perspective, another method would be to extend the population model simulations used in estimating B_{best}, the Scenario-Based Model of Eel Production II (SMEP II) (Aprahamian et al. 2007; Walker et al. 2013), downstream to the seaward boundary of the basin. The model simulations used to assess eel production for the UK 2012 EMP Review (Defra 2012) were based on data for yellow stage eels, because data on glass eel recruitment were lacking. As

a consequence, the simulations were limited to the freshwater compartment of the river basin, with production rates subsequently being extrapolated to the estuarine compartment. Extending those simulations downstream to include the estuaries where glass eel fisheries operate would facilitate a more direct assessment of the potential impact of those fisheries. Furthermore, at present, the estimate of the maximum potential production (B_{best}) from any eel index river basin is a temporally static assessment, in that it estimates silver eel production in the same year that the yellow eel surveys were undertaken. The population model (SMEP II) used for England and Wales assessment does have the capability to forecast the silver eel production in future years. However, in the absence of a simulated annual recruitment, the predicted silver eel escapement will inevitably decline year after year as eels in the modelled population either 'silver and emigrate', or 'die'. The knowledge required to simulate a locally relevant quantity of glass eel recruitment would allow the impact of glass eel catches on future silver eel production to be predictively forecast.

Summary

The behavioural processes, abiotic environmental variables and hydrodynamic factors governing the distribution and abundance of glass eels in estuaries are clearly very complex, with interactions between many of these variables also serving to further confound temporal and spatial distribution patterns. However, it is important to understand the behavioural mechanisms utilised by glass eels within estuaries in order to facilitate reliable estimation of yearly recruitment to the adult population and subsequent silver eel escapement from the river system.

This review has aimed to synthesise the current scientific knowledge on glass eel migratory behaviour within estuaries, along with briefly highlighting various approaches that have been used to estimate seasonal recruitment and how these data may be used in assessing local production. These techniques could, in theory, be translated to any estuary system, with suitable sampling stations being selected based on hydrodynamic influences. However, although the general behaviour of glass eels in estuaries is reasonably well understood, site specific factors are likely to

play a significant role in determining finer scale distribution patterns and hence the efficacy and statistical robustness of any sampling procedure.

The innate behavioural processes modulating the response of glass eels to environmental cues such as river flow, odour, light intensity and temperature are relatively well understood. However, the daily, seasonal and annual variability in the magnitude of these environmental cues mean that, for any given estuary system, extrapolating often limited survey data to annual abundance estimates can be difficult. Furthermore, applying models of glass eel recruitment across different estuary systems can be problematic due to the variation in environmental conditions and the often subtle effects these can have on glass eel distribution patterns.

In addition, estimating recruitment at the estuary mouth is further confounded, not by methodological issues; rather, by the significant resource commitment necessary to adequately sample in these locations. The under-dispersed nature of glass eel distribution in coastal areas means that a large number of temporally and spatially distributed samples would be required to robustly monitor fluxes entering the estuary mouth.

With this in mind, behavioural studies on a site-by-site basis would likely be required in order to elucidate temporal and spatial (both horizontal and vertical) distribution patterns specific to particular estuaries and river systems of interest. These studies would help to inform future monitoring strategies, with a view to optimising the large resource commitment required to accurately estimate the abundance of this critically important and vulnerable ontogenetic stage of anguillid species worldwide.

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