Current status and temporal trends in stocks of European eel in England and Wales

A. Bark, B. Williams, and B. Knights


An extensive 4-year programme of catchment surveys, data collection, and model development for eels was undertaken to establish the status of the stocks in England and Wales, so that appropriate management action can be taken. Nine test catchments representing different geographical areas and catchment types were studied, covering 14 rivers, two estuaries, and a fresh-water lagoon. Data were collected via electric fishing, fykenetting, fixed eel racks, and elver traps. In all, 13,500 eels were caught, weighed, and measured, and the sex and age of a subsample of 1400 determined. Despite declining recruitment, eel stocks in some, perhaps many, west coast rivers are probably still at or near to carrying capacity, with male-dominated populations. In other rivers, particularly those towards the southeast of England, current and historical data indicate declining female-dominated stocks. For rivers where recruitment is not limiting, there appears to be a direct relationship between the standing stock of eels and the mean nitrate level. This relationship potentially facilitates the application of a biomass-based biological reference point for eels for application to individual catchments. The data also suggest that it may be possible to develop reference points based on mean eel length or sex ratio.

Keywords: Anguilla anguilla, assessment, management, population, reference points, stocks.

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Introduction

Major declines in recruitment of glass eels since the late 1970s (Moriarty, 1996; Dekker, 2003) have led to concerns about stocks and fishery yields, and to the suggestion that the European eel population has reached a critically low level. According to landing statistics from the Food and Agriculture Organization of the United Nations (FAO), the population has declined dramatically since the early 1970s. This statement has been corroborated by data on recruitment and landings from the International Council for the Exploration of the Sea (ICES, 2006), which show a drastic decline from the end of the 1970s. Eel recruitment stabilized briefly during the 1990s, according to selected datasets (ICES, 2006) before declining to an apparently all-time low of some 1% of late-1970s levels, in 2001. However, in the UK, glass eel recruitment to the southwest-facing River Severn is estimated (from changes in commercial catch per unit effort, cpue) to have declined by ~70% since the peaks of the late-1970s and early 1980s (ICES, 2006), less than the estimates above. A recent review of data and time-series from across Europe has also shown that stocks may not have declined to the extent suggested by declines in landings, and that there have been comparable historical fluctuations in recruitment and stocks (Knights et al., 2006).

Licence sales in England and Wales have remained relatively constant, as have reported yellow and silver eel catches and catch rates measured as kilogramme per instrument of capture. Home (and European mainland) consumption continues to decline, and more than half the European demand now appears to be met by farmed and frozen eels. Catch values in £ per kg have declined in real terms since the 1980s, and fishers have been reducing fishing effort, although cpue and incomes in £ per instrument of capture have continued to fall. Therefore, export volumes and values in real terms have continued to decline, and economic factors may be an important contributor to the declining yields of eels, in addition to yellow eel stock decreases attributable to poor recruitment or overfishing (ICES, 2006).

A study “Eel and elver stocks in England and Wales: their status and management options” (Knights et al., 2001) was commissioned by the UK Government Agencies in 1997. The study recommended that stochastic life-stage compartmental modelling approaches could be a cost-effective means to aid future research and development, setting of management reference points, and monitoring. In response to those proposals, an extensive 4-year programme of catchment surveys, data collection, and model development of eels has been funded by the UK Department for Environment, Food and Rural Affairs (Defra), entitled “Establishment and implementation of biological reference points for the management of the European eel”. A key aim of this second study was to undertake detailed studies of a series of test catchments to establish the status of eel stocks in England and Wales, upon which appropriate management actions can be based. In addition, a Scenario-based Model for Eel Populations (SMEP) was developed to model the fresh-water phase of populations of the European eel in the UK (Aprahamian et al., 2007). It is based at the scale of a river catchment and considers both the biological characteristics of the eel population and
a number of potential anthropogenic influences on that population. Biological characteristics modelled include growth, natural mortality, sexual differentiation, maturation, and migration. Testing and refinement of the model continues.

Based on the data collected from the test catchments, the primary aim of this paper is to summarize the current status and temporal trends in stocks of the European eel in England and Wales, in relation to such factors as population density, sex ratio, habitat carrying capacity, and distance from the continental shelf. Second, the eel data are used to explore the potential for setting catchment-based biological reference points for eel stock status and how such reference points might be monitored. The need for such reference points has been accepted, de facto, by the European Commission, whose proposed Eel Recovery Plan (CEC, 2005, 2006) sets a silver eel escapement target (target reference point) of 40% of the biomass that would be expected in a pristine state, i.e. in the absence of anthropogenic impact.

**Test catchment selection and characteristics**

Nine test catchments were surveyed (Figure 1). Different areas and catchment types have been studied, covering 14 rivers, one estuary, one tidal lagoon, and one fresh-water lagoon. The choices included at least one catchment per River Basin District (except Southern), fished and unfished systems, and minimally impacted to heavily modified waterbodies (there being no truly pristine rivers in England and Wales).

The location of the test catchments was determined by several factors. The first was to match the location of previous surveys for the River Severn (Aprahamian 1986, 1988; Knights et al., 2001), River Piddle, and River Frome (Morrice et al., n.d.; Knights et al., 2001), to allow for continuity of datasets. Replication of the surveys allowed for the identification of trends in the data and/or temporal changes in the population structure. The second requirement was to cover a range of catchment types (oligotrophic mountain streams to eutrophic lowland rivers), and the third to achieve a geographical spread around the coastline to reflect different distances from the edge of the continental shelf (Figure 1).

Table 1 summarizes the key physical characteristics of the test catchments, including their approximate distance from the edge of the continental shelf (DCS), river length, and trophic status. DCS is included because this is representative of relative distances from the main Atlantic leptocephalus migration pathways to catchments, and hence potentially to different levels of successful recruitment of glass eels. Mean nitrate levels have been used as an indicator of trophic status and/or productivity. Nitrate levels can be expected to reflect both natural catchment geology and anthropogenic inputs, and nitrate data are readily available for almost any river in the UK.

The following points and relationships should be noted regarding the test catchments. The River Severn, at some 350 km long, is the UK’s longest river. However, those data presented here relate to small, mostly lowland tributaries draining to the upper part of the tidal estuary. The rivers Start and Gara are the principal feeder streams to Slapton Ley, a shallow (maximum winter depth 3.1 m) eutrophic fresh-water lagoon of some 75 ha, separated from the sea by a shingle ridge. The outlet stream from Slapton Ley drains directly to the sea across the shingle beach. The River Wnion in North Wales drains to the sea via the Mawddach Estuary. The Tadnoll Brook is a tributary of the River Frome. Both the Frome and the Piddle drain to the western end of Poole Harbour, a large (ca. 36 km²), shallow, saline, tidal lagoon. The Rivers Colne and Blackwater (in Essex) are two adjacent rivers draining to the southern North Sea. They are considered as a single unit for much of the following discussion. Eel data provided by the Environment Agency relate to both the Colne and Blackwater and two additional Essex rivers, the Chelmer and the Stour.

**Data collection and analysis**

Data were collected by electric fishing, fykenetting, fixed eel racks, and elver traps, depending on which life stage was being targeted (Table 2) and the type of waterbody being surveyed (Table 1). Eel-specific electric fishing methods were followed as outlined in Knights et al. (2001), particularly a minimum of three passes per site and slow progression up the survey stretch. To ensure that small eels were sampled adequately, D-nets of 3 mm mesh were deployed. Electric fishing sites consisted of some 100 m of channel selected to contain the range of habitats typical of the area. Electric fishing was completed in the optimum period of May–September (Knights et al., 1996), and repeat surveys were carried out at the same sites and times of year [Rivers Severn and Piddle, and Tadnoll Brook (River Frome)]. In each catchment (except the Severn), 15–22 survey sites were fished. Considerable care was taken to ensure that sites were distributed as evenly as possible throughout each system to allow valid comparison of population parameters between rivers, and to avoid potential upstream/downstream bias. For the lower Severn tributaries, 24 sites were fished in 1998 and 16 in 1999 (Knights et al.,
Table 1. Physical variables for the test catchments.

<table>
<thead>
<tr>
<th>Catchment</th>
<th>Geographical location</th>
<th>DCS a (km)</th>
<th>Length (km)</th>
<th>Altitude at source (m)</th>
<th>Trophic status (nitrate, mg l⁻¹)</th>
<th>Man-made barriers</th>
<th>Natural barriers</th>
<th>Habitat type</th>
<th>Eel fishing</th>
</tr>
</thead>
<tbody>
<tr>
<td>River Blyth</td>
<td>Northeast</td>
<td>465</td>
<td>40</td>
<td>210</td>
<td>13.46</td>
<td>Yes</td>
<td>No</td>
<td>Largely natural lowland river</td>
<td>None</td>
</tr>
<tr>
<td>River Darent</td>
<td>Southeast</td>
<td>850</td>
<td>40</td>
<td>100</td>
<td>21.29</td>
<td>Yes</td>
<td>No</td>
<td>Modified chalk river</td>
<td>None</td>
</tr>
<tr>
<td>River Ellen</td>
<td>Northwest</td>
<td>420</td>
<td>30</td>
<td>400</td>
<td>13.61</td>
<td>Yes</td>
<td>No</td>
<td>Largely natural upland river</td>
<td>None</td>
</tr>
<tr>
<td>River Colne</td>
<td>Southeast</td>
<td>850</td>
<td>17</td>
<td>90</td>
<td>43.7</td>
<td>Yes</td>
<td>No</td>
<td>Eutrophic lowland river</td>
<td>None</td>
</tr>
<tr>
<td>River Blackwater</td>
<td>Southeast</td>
<td>850</td>
<td>35</td>
<td>90</td>
<td>43.7</td>
<td>Yes</td>
<td>No</td>
<td>Eutrophic lowland river</td>
<td>None</td>
</tr>
<tr>
<td>River Hull</td>
<td>East</td>
<td>0.650</td>
<td>40</td>
<td>25</td>
<td>40.13</td>
<td>Yes</td>
<td>No</td>
<td>Highly modified lowland river</td>
<td>None</td>
</tr>
<tr>
<td>River Piddle</td>
<td>South</td>
<td>460</td>
<td>30</td>
<td>130</td>
<td>33.46</td>
<td>Yes</td>
<td>No</td>
<td>Semi-natural chalk river</td>
<td>Silver trap</td>
</tr>
<tr>
<td>Severn upper estuary/lowland tributaries</td>
<td>Wales</td>
<td>490</td>
<td>10–30</td>
<td>100</td>
<td>25.8</td>
<td>Yes</td>
<td>No</td>
<td>Predominantly lowland semi-natural streams</td>
<td>Glass eel</td>
</tr>
<tr>
<td>Rivers Start and Gara b</td>
<td>South</td>
<td>370</td>
<td>10–15</td>
<td>140</td>
<td>14.8</td>
<td>Yes</td>
<td>No</td>
<td>Small unmodified hill streams</td>
<td>None</td>
</tr>
<tr>
<td>Tadnoll Brook c</td>
<td>South</td>
<td>460</td>
<td>10</td>
<td>40</td>
<td>24.94</td>
<td>Yes</td>
<td>No</td>
<td>Lowland chalk stream</td>
<td>None</td>
</tr>
<tr>
<td>River Wnion</td>
<td>NW Wales</td>
<td>510</td>
<td>30</td>
<td>750</td>
<td>2.22</td>
<td>No</td>
<td>Yes</td>
<td>Natural, oligotrophic mountain river system</td>
<td>None</td>
</tr>
<tr>
<td>Mawddach (Wnion) Estuary</td>
<td>NW Wales</td>
<td>510</td>
<td>–</td>
<td>–</td>
<td>2.67</td>
<td>No</td>
<td>–</td>
<td>Tidal estuary</td>
<td>None</td>
</tr>
<tr>
<td>Poole Harbour</td>
<td>South coast</td>
<td>460</td>
<td>–</td>
<td>–</td>
<td>23.78</td>
<td>No</td>
<td>–</td>
<td>Tidal lagoon</td>
<td>Fykenets</td>
</tr>
<tr>
<td>Slapton Ley</td>
<td>Southwest coast</td>
<td>370</td>
<td>–</td>
<td>–</td>
<td>38.18</td>
<td>Yes</td>
<td>–</td>
<td>Fresh-water coastal lagoon</td>
<td>None</td>
</tr>
</tbody>
</table>

aDistance from Continental Shelf (migration pathways).

bFeeder streams to Slapton Ley, Devon.

cTributary without barriers off the River Frome (48 km long), Dorset, that does have minor barriers.

2001), all of which corresponded as closely as possible to the sites used by Aprahamian in 1983/1984 (Aprahamian, 1986, 1988). In all, 13 lower Severn sites were fished in 2002, 2003, and 2004, nine of which were common to all survey years from 1983 to 2004. Basic physico-chemical data were also collected at each electric fishing site.

Commercial double-ended fykenets (55 cm opening, 10 mm mesh, 6 m leader) were used in the estuary and lake waterbodies (Mawddach estuary, Poole Harbour, Slapton Ley). Nets were set in strings of up to five double-ends in the early evening, and retrieved the following morning. Size selectivity of fykenets has been well documented (Naismith and Knights, 1990; Tesch, 2003). The nets employed effectively retained eels > 300 mm, so samples allowed cpe, sex, and age data to be collected.

Silver eel racks on the Rivers Frome and Piddle were run by local fishers between September and December, on nights suitable to maximize the catch of migrating silver eels. The eel racks had a 10-mm-wide bar spacing to ensure that all eels, including the smallest migrating males, were caught. Samples were obtained through the season to avoid any bias in sex ratios arising from the possible tendency for males to migrate earlier than females.

In partnership with the Westcountry River Trust and Slapton Ley National Nature Reserve, two elver ladder traps (Solomon and Beach, 2004a, b) were installed to sample recruiting eels at the outflow weir of Slapton Ley, which discharges directly onto the shingle beach and into the English Channel. The traps were run between April and July of 2005 and 2006, until water levels in the ley fell below the outflow.

Eel age was determined by burning and cracking the sagittal otoliths (Moriarty, 1973), following the protocol of Byatt and Harrison (n.d.). Growth rate (mm y⁻¹) was calculated from length minus 70 mm divided by age. It is widely recognized that different methods of otolith preparation yield different ages, and that these differences may be compounded by operator bias (Tesch, 2003). Therefore, comparisons of relative growth rate and population turnover between the catchments within the current dataset are valid, but absolute comparisons with other datasets are potentially problematic.
Table 2. Summary of mean biological characteristics of the eel population in the test catchments, and survey details.

<table>
<thead>
<tr>
<th>Catchment</th>
<th>Density (number m(^{-2}))</th>
<th>Biomass (g m(^{-2}))</th>
<th>Mean length (mm)</th>
<th>Sex ratio (% female)</th>
<th>Growth rate (mm year(^{-1}))</th>
<th>Survey method</th>
<th>Targeted life stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>River Blyth u/s(^a)</td>
<td>0.05</td>
<td>1.99</td>
<td>211</td>
<td>35</td>
<td>19.9</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>River Blyth d/s(^a)</td>
<td>0.96</td>
<td>16.22</td>
<td>191</td>
<td>–</td>
<td>–</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>River Darent</td>
<td>0.04</td>
<td>9.34</td>
<td>477</td>
<td>98</td>
<td>28.2</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>River Ellen</td>
<td>0.29</td>
<td>6.79</td>
<td>93</td>
<td>41</td>
<td>18.9</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>River Colne</td>
<td>0.11</td>
<td>9.96</td>
<td>352</td>
<td>85</td>
<td>20.2</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>River Blackwater</td>
<td>0.07</td>
<td>9.65</td>
<td>615</td>
<td>85</td>
<td>24.5</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>River Hull</td>
<td>0.03</td>
<td>6.54</td>
<td>396</td>
<td>88</td>
<td>21.4</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>River Piddle</td>
<td>0.08</td>
<td>12.39</td>
<td>416</td>
<td>94</td>
<td>20.2</td>
<td>Electric fishing/eel trap</td>
<td>Yellow/silver</td>
</tr>
<tr>
<td>Severn upper estuary/lowland tributaries</td>
<td>0.49</td>
<td>15.01</td>
<td>212</td>
<td>5</td>
<td>15.9</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>Rivers Start and Gar(^a)</td>
<td>0.11</td>
<td>0.47</td>
<td>250</td>
<td>58</td>
<td>18.6</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>Tadnoll Brook(^c)</td>
<td>0.27</td>
<td>15.09</td>
<td>284</td>
<td>51</td>
<td>19.3</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>River Wnion</td>
<td>0.15</td>
<td>3.89</td>
<td>265</td>
<td>11</td>
<td>18.4</td>
<td>Electric fishing</td>
<td>Yellow</td>
</tr>
<tr>
<td>Mawddach (Wnion) estuary</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.4</td>
<td>131</td>
<td>360</td>
<td>31</td>
<td>24.5</td>
<td>Fykenet</td>
<td>Yellow</td>
</tr>
<tr>
<td>Poole Harbour</td>
<td>2.8</td>
<td>518</td>
<td>439</td>
<td>98</td>
<td>40.4</td>
<td>Fykenet</td>
<td>Yellow</td>
</tr>
<tr>
<td>Slapton Ley</td>
<td>1.8</td>
<td>328</td>
<td>448</td>
<td>88</td>
<td>26.7</td>
<td>Fykenet, eel trap</td>
<td>Elver/Yellow</td>
</tr>
</tbody>
</table>

\(^{a}\)Upstream (u/s) and downstream (d/s) of a migration barrier, see text for further explanation.

\(^{b}\)Feeder streams to Slapton Ley, Devon.

\(^{c}\)Tributary of River Frome, Dorset.

Sex of individual eels was determined by macroscopic examination of the gonads, with ambiguous cases confirmed by microscopic examination of gonadal smears with guidance from Sinha and Jones (1966) and Tesch (2003). Yellow eels for sex determination were selected on a stratified random basis, based on 50-mm size classes from 250 to 500 mm taken from across the catchment. All eels >500 mm were assumed to be female, and 250 mm was taken as the lower limit at which sex could be determined. The sex ratio (% female) for each catchment could then be calculated based on the proportional representation of each size class within the population. Silver eel sex ratios were based on size, with all eels >450 mm assumed to be female. Gonad examination of a sample of silver eels 400–500 mm long confirmed that any error arising from this assumption was not significant.

In all, 13 500 eels (excluding Slapton eel trap catches) were caught, and their length and weight recorded, and a subsample of 1400 was subjected to analysis of sex and age. Data were collated and analysed in Microsoft Office Excel 2003.

**Results and discussion**

**Current stock status**

Eel catch data for the various catchments are summarized in Table 2 and Figures 2 and 3. Eels were present in all the systems and, although population densities varied greatly, there was a clear generalized spatial trend. Population densities were highest in western and northeastern rivers, and lowest in southeastern and eastern rivers, the pattern clearly reflecting different levels of recruitment in relation to distance from the edge of the continental shelf (Table 1). As glass eels could either migrate to east coast catchments via the English Channel or around the north of Scotland, in some instances here, distances are based on the strongest transport currents rather than the shortest distance. However, two rivers stand out as having lower population densities than expected, the Rivers Piddle and Hull.

The Hull is a particularly complex and highly modified river. A major part of the catchment is very low-lying, and water levels and drainage are controlled by an extensive system of sluices and pumps which render ingress of eels, and in some parts egress, difficult. Furthermore, the large expanse of the Humber Estuary, into which the River Hull drains, provides an extensive area of accessible habitat, potentially lessening density-dependent pressures for up-river migration (Feunteun et al., 2003). Qualitative sampling of a small stream which drains directly to the North Sea a few kilometres north of the Humber Estuary revealed very large numbers of elvers (young of the year) and small eels, supporting the view that a shortage of recruits in this region of the North Sea may not be the primary reason for poor recruitment into the River Hull.

Like the River Hull, the River Piddle drains to a large productive tidal system that potentially acts as a sink for many of the available recruits (Knights et al., 2001). Recruitment to the Piddle is discussed further below, in relation to temporal changes.

It is apparent from Figure 2 that biomass does not follow the same pattern as population density. For the high-recruiting rivers, e.g. the Severn tributaries and the Ellen, high population
densities are reflected in high biomass. However, there is a clear tendency for the low-recruiting rivers of low population density, e.g. the Colne and the Blackwater in Essex, the Piddle, the Hull, and the Darent, to maintain a relatively high biomass, a clear reflection of the greater mean length of eels in the population (Table 2). This relates to the tendency for density-dependent sex determination, i.e. lower recruitment leading to lower densities but higher proportions of larger females (Parsons et al., 1977; Davey and Jellyman, 2005).

Population structure is illustrated further in Figure 3, which splits the population of each river system into four size classes: up to 250 mm (young undifferentiated into sex); 251–350 mm (sexually differentiated immature males and females); 351–450 mm (male prespawners and immature females); >450 mm (female prespawners). Figure 3 shows a clear dichotomy between high- and low-recruiting rivers, with starkly opposing population structures. The high-recruiting (west and northeast) rivers show a classic structure for a stable population, with numbers of individuals decreasing approximately exponentially with increasing size. In contrast, the low-recruiting rivers (Hull, Darent, Piddle, and the Essex rivers) show a population that is heavily dominated by larger (mostly female) eels, and an acute shortage of the smallest size classes. The Tadnoll Brook shows an intermediate population structure.

Taken at face value, the relative lack of eels in the smallest size classes in the low-recruiting rivers suggests that recruitment is in a state of active and potentially severe decline. Although this conclusion accords with the accepted picture of glass eel recruitment to Europe, it presupposes that recruitment to the rivers is always dominated by elvers. There is increasing evidence from Ca/Sr otolith studies that anguillid eels display a wide range of facultatively catadromous behaviour, and that yellow eels may enter or leave fresh water at any stage, or indeed remain permanently in estuarine or coastal waters (Tzeng et al., 1997; Tsukamoto and Arai, 2001; Arai et al., 2003; Jessop et al., 2006). In this context, the Slapton Ley elver traps provided some potentially interesting data. Some 5000 eels were trapped between April and July 2006, and the length-frequency distribution of eels >70 mm is shown in Figure 4. Approximately half the catch consisted of partly pigmented elvers, and the other half older eels up to 420 mm long, the mode being 160–180 mm. As noted previously, the Slapton traps are located on the outflow to the Ley, which drains directly to the sea, with no intervening estuary. Although otolithometry has not yet been used to investigate whether these older eels are all first-time fresh-water immigrants, the Slapton trap data do suggest the potential importance of later stage recruitment in maintaining fresh-water stocks, particularly in view of their lower expected mortality in comparison with smaller recruits (Moriarty, 1986; Feunteun et al., 2003).

In considering the overall status of eel populations in the test catchments, it is also important to consider the impacts of fishing mortality, migration barriers, and carrying capacity, and the combined effects of physical and recruitment constraints on silver eel output and sex ratio. None of the rivers supports significant fisheries for yellow eels. As shown in Table 1, all but one of the river systems (River Wnion) have man-made structures that potentially form migration barriers. In most cases, these are low weirs that appear to have minimal impact on upstream migration. As already mentioned, there are major migration barriers on the River Hull. The Essex rivers (Colne and Blackwater) also have tidal structures that are probably a significant impediment to eel entry. A particularly clear barrier effect is apparent on the River Blyth, where there is a major weir a few kilometres from the tidal limit. Recorded mean population densities were 0.96 eels m$^{-2}$ below the weir but 0.05 m$^{-2}$ above it, with eels relatively uniformly spread throughout the rest of the catchment.

Only the River Wnion, a North Wales high-gradient mountain stream, contains significant natural migration barriers and no man-made barriers, with many seemingly impassable waterfalls and cascades on almost all the tributaries. Nevertheless, eels were distributed throughout the catchment, with at least small numbers to above 500 m elevation, indicating the extreme strength of the upstream migration urge of at least some members of the population.
Reliable historical data are available for three of the test catchments, the upper estuary tributaries of the Severn, and the Piddle and Essex rivers. Extensive eel surveys were undertaken throughout the Severn catchment in 1983/1984 by Aprahamian (1986, 1988). Additional more-restricted surveys were undertaken in 1998 and 1999 (Knights et al., 2001). The outbreak of Foot and Mouth Disease across England and Wales in 2001 inhibited glass eel fishers reaching the banks of the River Severn and other fishing sites. As a result, it was estimated that glass eel fishing effort was reduced by up to 70% (Peter Wood, UK Glass Eels, pers. comm.). In light of this, it was decided to focus resources on a limited number of survey sites (13) on the upper estuary tributaries in 2002, 2003, and 2004, to assess the impact of reduced fishing effort in 2001, rather than re-surveying the entire system as in previous surveys. A major eel survey of the River Piddle was undertaken in 1976/1977 (Morrice et al., n.d.) and further detailed surveys in 1999 (Knights et al., 2001) and 2003/2004. The rolling programme of multispecies fish surveys conducted using constant methodology by the Environment Agency on the Essex rivers (Colne, Blackwater, Chelmer, and Stour) from 1984 to 2005 placed specific emphasis on eels, and provides a valuable 21-year dataset (Ros Wright, Environment Agency, pers. comm.).

Figure 5 shows the mean population density of eels for the nine River Severn upper estuary tributary sites that were common to all survey years (1983–2004). There is no indication of a long-term trend in population density, although there is obvious interannual variability. The apparent decline of ~25% between 1998 and 1999 is statistically significant (paired \( t \), \( p = 0.01 \)), but densities have been relatively high subsequently. This almost certainly reflects natural spatiotemporal variability between years and illustrates one of the difficulties of conducting and interpreting eel surveys. The biomass and population structure data (not illustrated here) also support the hypothesis of no long-term trend. Therefore, although glass eel recruitment to the Severn system as a whole may have declined by ~70% from its peak in the late 1970s (Introduction), it would appear that recruitment is still sufficient...
to meet local carrying capacity in the upper estuary tributaries. There was no indication of an enhanced 2001 cohort (year of the reduced glass eel fishery because of the Foot and Mouth restrictions), suggesting that the River Severn glass eel fishery has minimal impact on local eel stocks, a conclusion also reached by Knights et al. (2001).

Figure 6 illustrates temporal changes in population density and population structure in the River Piddle. There has clearly been a major decline in population density between the mid-1970s and today. This has been accompanied by a profound change in population structure, from one dominated by small eels to one currently dominated by large eels, clearly suggestive of a major recruitment failure. Sex ratio, based on an analysis of catches of silver eels, has changed from 2.7:1 male:female in 1976 to ~0.05:1 male:female in 2003/2004. Although output of male silver eels from the River Piddle has now almost ceased, current female silver eel output, and hence potential egg production, is actually higher than in the 1970s. This may have effectively offset the negative impacts of an overall decline in the stock, at least in the short term.

In contrast to the River Piddle, the eel population structure in Tadnoll Brook, a tributary of the River Frome (Figure 3), indicates that small eels still recruit to the Frome, though not in particularly large numbers. Why these two adjacent rivers should display major differences in their eel populations is wholly obscure, given that they are of essentially similar character, lack significant migration barriers, and share a common discharge point to Poole Harbour. The differences do, however, illustrate the highly variable and unpredictable behaviour of the European eel.

Figure 7 depicts the Environment Agency multispecies survey data for eels aggregated for four Essex rivers (Chelmer, Blackwater, Colne, and Stour). There is a clear and statistically significant (Pearson, \( p < 0.003 \)) decline in population density over the 21-year period 1984–2005. Mean eel population densities recorded from the multispecies surveys were 0.0052 m\(^{-2}\) for the Colne in 2002 and 0.007 m\(^{-2}\) for the Blackwater in 2003. These densities are an order of magnitude less than the eel densities of 0.11 and 0.07 m\(^{-2}\) recorded from the 2004 eel-specific surveys that formed part of the current study. Such stark differences in eel population estimates derived from multispecies and eel-specific surveys present major difficulties when comparing eel datasets from different sources (Knights et al., 2001).

The three temporal datasets provide some valuable insights into the current status of eel stocks in England and Wales. From the analyses presented here and despite a Europe-wide decline in glass eel numbers since the 1980s, it appears that recruitment to the upper estuarine tributaries of the River Severn, and probably other west coast and northeastern catchments, is still more or less sufficient to meet local carrying capacity, provided there is an absence of compounding factors such as migration barriers. For the River Piddle and the Essex rivers, there is clear evidence for a long-term decline of river eel stocks. As illustrated for the Piddle, this may initially lead to an increase in female silver escapement. However, the current population structure implies that there will be a major decline in output of female silver eels within the next few years, unless river populations are maintained by older immigrants from Poole Harbour. Although there is increasing evidence that such delayed migration to fresh water may be a common phenomenon (Tseng et al., 1997; Tsukamoto and Arai, 2001; Arai et al., 2003), it is unclear whether this would be sufficient to maintain stable river populations. Despite direct evidence of eel population decline within the study catchment set being limited to the Piddle and the Essex rivers, population structure in those two catchments is almost identical to that in the Rivers Hull and Darent, suggesting that a decline in river stocks could be widespread, particularly towards the southeast and east of England.

Taken together, the observations above suggest that eel populations in the west coast and possibly also northeastern rivers are probably at or near carrying capacity, at least where migration barriers are absent. In contrast, populations in the low-recruiting rivers, typically those towards the southeast of England, would appear currently below their potential carrying capacity. It can also be seen from Table 2 that there is a clear relationship between sex ratio and population density. The high-recruiting
rivers (Wnion, Severn tributaries, Ellen, and Blyth) are male-dominated, whereas the low-recruiting rivers (Piddle, Darent, Hull, and the Essex rivers) are heavily female-dominated. These last rivers are also the most productive and support faster growth rates. They are therefore of potentially greatest value to the species.

The current surveys also demonstrate the potential importance of standing waterbodies and estuaries to local stocks. Although it is not generally practical to obtain quantitative data on stock densities in large open systems, data on growth rate and sex ratios are relatively straightforward to collect. Pykenet samples were obtained for Slapton Ley, the Mawddach estuary, and Poole Harbour (Tables 2 and 3). In all three, eel growth rates were greater than in the inflowing rivers, markedly so for the River Piddle (20.2 mm year\(^{-1}\)) and Poole Harbour (40.4 mm year\(^{-1}\)), into which it flows. In all three cases, the percentage of females was greater than in the inflowing rivers and streams, confirming their importance to the spawning stock. This accords with the favourable growth conditions commonly found in stillwaters and estuaries (Oliveira et al., 2001; Daverat et al., 2006).

### Management implications and the development of biological reference points

The European Commission is currently developing an Eel Recovery Plan (CEC, 2005, 2006), which proposes that Member States be required to set up national eel management plans for each River basin District, “to permit with high probability the escapement to the sea of a high percentage of the biomass of adult eel relative to the best estimate of the potential escapement from the river basin, taking into account all the human activities affecting the fishing area or the stock”. A silver eel escapement target of 40% of the biomass expected in the pristine state, i.e. in the absence of anthropogenic impact, is proposed. There are two clear requirements for the application of this proposal: first, a measure or estimate of pristine state escapement, and second, a measure or estimate of current escapement. Provision of both may prove problematic.

The eel survey programme reported here provides a valuable overview of the current status of eel stocks in England and Wales. The data also illustrate clearly that, for eels, spatiotemporal variability is high and that it is very difficult to define a typical waterbody or a typical eel population. Therefore, to develop a single management approach or target reference point that incorporates the full range of eel habitats, i.e. streams, rivers, lakes, coastal lagoons, estuaries, and coastal waters, is difficult. Although the proposed European Commission target relates to silver eel escapement, direct measurement of escapement will rarely be a practical proposition, especially in estuarine or marine habitats, so proxy measures will be required. The most obvious predictor for silver eel escapement will be the yellow eel standing stock, measured in terms of either population density or biomass. At a basic level, more yellow eels can be expected to produce more silver eels.

The maximum eel standing-stock biomass will be a function of carrying capacity, but defining and assessing the carrying capacity of a system for eels is problematic and is likely to encompass a range of variables. Although the potential value of Habitat Suitability Indices for eels has been recognized (ICES, 2004), practical indices have yet to be developed (Knights et al., 2001). However, given the apparently highly catholic nature of an eel’s habitat requirements, trophic status might be expected to provide an approximate guide to potential carrying capacity. As shown in Table 1, there is considerable variation in nitrate levels (UK Environment Agency, GQA routine monitoring data) for the different river systems. Nitrate levels are typically lowest in the high-recruiting rivers (with the exception of the Severn tributaries), and dramatically so in the River Wnion, which correlates with its overall relatively low eel population density and biomass. In contrast, the low-recruiting rivers are typically lowland ones that are more productive and therefore potentially have the greatest carrying capacity.

Figure 8 represents an attempt to define carrying capacity in terms of river productivity, as represented by mean nitrate level. Eel biomass is plotted against nitrate for those English and Welsh rivers where it is reasonable to assume that eel populations were more or less at carrying capacity, and datasets are compatible, i.e. derived from intensive eel-specific surveys. These are: Lower Severn tributaries 2002–2004; Wnion 2004; Ellen 2004; Start and Gara 2005 (all from the current study); and the Tadnoll Brook in the 1970s (data from Mann and Blackburn, 1991); Piddle 1976/1977 (data from Morrice et al., n.d.; Knights et al., 2001); Welsh Dee in 1984 (Aprahamian, 1988; a repeat survey in 1998 showed no change; Knights et al., 2001).

Figure 8 establishes a clear relationship between presumed maximum eel biomass (carrying capacity) and nitrate level. Clearly, this relationship should be regarded as tentative given...
the rather small sample size, but it provides a potential mechanism for establishing a pristine-state biomass reference level for data poor rivers, and therefore for comparing actual and expected population biomass. If it is assumed that standing-stock biomass can be used as a proxy for silver eel escapement biomass, then compliance with an escapement target should be straightforward, as illustrated in Table 3. This suggests that all of the low-recruiting rivers in the study set are underperforming, and that the River Hull and the Essex rivers would fail to meet the proposed EU target of 40% silver eel escapement relative to pristine state. The River Piddle appears to reach the target (in terms of silver eel biomass production), but is predicted to fail on escapement, with an estimated silver eel trap take of 25–30% of emigrants.

Considering eel populations on a whole-catchment basis is appropriate for the relatively short rivers that constitute the study set. In the absence of migration barriers, the eel population is distributed throughout the catchment, and biomass does not decline markedly with distance upstream. Any decrease in numbers tends to be offset by an increase in average size. For large (long) rivers, however, a decline in biomass with increasing distance upstream from the tidal limit is inevitable. The reference condition model (RCM) (Aprahamian et al., 2007) allows comparison of the observed and expected declines with increasing elevation or distance from the tidal limit.

There are, however, significant practical constraints with using biomass (or population density) as an indicator of population status. First, datasets must be compatible, which demands both standardized and consistent data-collection methodology. This point is well illustrated by the Environment Agency data for the Essex rivers discussed earlier. Those data are excellent for temporal trend analysis, because they were collected in a consistent manner over a period of 21 years. However, they are less helpful for assessing actual stock status. Mean eel population density recorded from the Agency’s multispecies surveys of the Colne and Blackwater were an order of magnitude lower than the densities recorded from the 2004 eel-specific surveys that formed part of the current study. The difficulties in surveying eel populations successfully, even in small catchments, and the lack of comparability between datasets obtained by different survey methods and teams, coupled with the resource requirements for carrying out large numbers of eel-specific surveys, may limit the use of standing-stock biomass as a tool for assessing reference point compliance. Moreover, for large, deep rivers, large lakes, and estuaries, there is no practical method for measuring biomass or population density.

There may also be a temporal issue with the use of biomass as an indicator. Eels <300 mm typically contribute 10–25% of the population biomass. Therefore, it might be 10 years or more before a major change in recruitment is reflected in a readily measurable and statistically confirmable change in biomass. In contrast, changes in length frequency distribution as a result of changes in recruitment or fishing pressure may be more sensitive, and are certainly easier to detect and to corroborate statistically.

Figure 9 depicts the relationships between population density (mean of all survey sites in catchment), average eel length, and sex ratio (% female), using data from the test rivers. and moreover that the correlations are quite strong. The rivers in the set where mean eel length is high (>350 mm) and the proportion of females is very high (>85%) are those suggested in Table 3 to be at least than carrying capacity for eels (the Darent, Tadnoll Brook, the Blythe, the Piddle, the Hull and the Essex rivers). This suggests that the mean length or sex ratio of a random sample of eels from across the catchment (or from a reach of a large catchment) could potentially provide a direct measure of stock status and might therefore form the basis of an eel stock reference point.

Clearly, the number of rivers in the dataset is quite small, so it has yet to be shown that the foregoing putative relationships are acceptably robust. In particular, the explicit form of the relationship between sex determination and density-dependence has yet to be established. However, although the current study suggests that a biomass reference point based on mean nitrate levels appears feasible, there would be clear practical advantages to a mean length or sex-based reference point for target or compliance monitoring. The principal advantage would the relative ease of obtaining the required monitoring data, because only random samples rather than quantitative surveys would be required. Therefore, for a given level of resource, useful data could be obtained for a much larger number of catchments, which brings
obvious monitoring and management advantages. Standardized sampling would still be required to ensure that the sample was representative of the size structure of the population and that smaller eels were not missed (D-nets of 3-mm mesh were used for the electric fishing surveys reported here). Second, a random-sample-based reference point is potentially applicable to all environments, including large rivers, estuaries, lakes, and coastal waters, where quantitative surveys are effectively precluded. Fyke nets, depending on mesh size, will retain eels >250 or 300 mm (the approximate size limit for straightforward sex determination), and allow the sex ratio of the population to be determined by the method used here. Mean length, though excluding eels below the retention cut-off, can also be determined.

Conclusions

The data collected from the test catchments suggest that despite a continent-wide decline in recruitment, eel stocks in some, perhaps many, rivers along the west coast of England and Wales are probably still at or near carrying capacity, with male-dominated populations. This may also apply to some rivers in the northeast of England. For other rivers, particularly those towards the southeast of England, current population structure and the limited historical data suggest that eel populations have declined in recent decades, and are likely to decline further. Eel populations are heavily female-dominated. Although increased distance from the edge of the continental shelf can be expected to limit recruitment naturally towards southeast England, failure to meet carrying capacity is often exacerbated by tidal and other flood control structures, which restrict immigration.

For rivers where recruitment is apparently not limiting, there appears to be a direct relationship between eel standing-stock biomass and mean nitrate level. This relationship potentially facilitates the application of a biomass-based biological reference point for eels at the level of an individual catchment. The test catchment data also suggest that it may be possible to develop reference points based on mean eel length or sex ratio. Use of these measures would have the advantage of relative ease in collecting the required monitoring data, and potential applicability to habitats where electric fishing is precluded, such as estuaries and coastal waters. Further research to develop practical reference points is required, because forthcoming EU and national eel management policies will require assessment of stocks in relation to escapement targets.

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References


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