EELS (*ANGUILLA ANGUILLA* (L.)) OF THE LOWER RIVER SHANNON, WITH PARTICULAR REFERENCE TO SEASONALITY IN THEIR ACTIVITY AND FEEDING ECOLOGY

**P. Cullen and T.K. McCarthy**

**ABSTRACT**

The general biology and seasonal ecology of eels from a riffle section of the lower reaches of Ireland’s largest river system, the River Shannon, were investigated. Eels at this location occurred in high densities, had a slow growth rate and were predominantly male at maturation. Although they fed to some degree all year round, foraging activity of the eels was highest in the months of May to September, inclusive. Their diet, which was dominated by larval Ephemeroptera and Trichoptera, reflected the typical composition of the macroinvertebrate species assemblage of the riffle habitat sampled. Little evidence of piscivory or of the potential impact of the high density eel population on the salmonid stocks of this river section was recorded.

**INTRODUCTION**

The European eel *Anguilla anguilla* (L.) population has declined strongly throughout its range since the 1980s (Feunteun 2002). The causes of this decline are not clear, though it seems likely that several factors may be to blame, including loss of habitat, water quality problems, obstacles to migration, overfishing of all life history stages, introduced pathogens and perhaps also changes in oceanic conditions due to climate change. As a result there is an urgent need for research on the population biology of the species, at all stages in its typically catadromous life cycle. Though many studies have been undertaken on the ecology of the eel in inland European waters, the vast majority of these have concentrated on lacustrine eel populations. Riverine population studies have often concentrated on stream studies or have been based on studies of the seasonal spawning migration of the mature component of the river system’s eel population.

The River Shannon, Ireland’s largest river system, like most European inland waterways, has been subject to various anthropogenic impacts (McCarthy and Cullen 2002). Its eel population has been affected by a steady decline in juvenile recruitment, although the effects may not be as extreme as experienced in many other European systems. The lower reach of the river, although subject to flow regulation since the late 1920s, is one of the remaining areas within the Shannon system that still harbours a relatively dense eel population.

In this paper we document the general population characteristics of a large, lower reach riffle section of the main river channel and describe variation in eel feeding ecology with particular reference to seasonality and effects of eel size.

**MATERIALS AND METHODS**

**STUDY AREA**

The study site was located on a riffle stretch of the lower reaches of the River Shannon, approximately 8km upstream of the tidal limit (Fig. 1). Flow rates on this stretch of river channel are generally low and well regulated at a statutory minimum flow of 10 m$^3$ sec$^{-1}$ as a result of the construction of the Ardnacrusha hydroelectric generating station and the associated Parteen regulating weir in the mid- to late 1920s. This regulating weir is located approximately 10km upstream of the study site. Although the bulk of the river’s waters are diverted at the regulating weir, via a headrace canal, to the power station, it is sometimes necessary in winter months to ‘spill’ water at the regulating weir down the main river channel. Although ‘spillage’ rates have been known on occasion to exceed...
600 m$^3$ sec$^{-1}$, this is the exception rather than the norm, and during the period of this study water was ‘spilt’ over a three week period in late February and early March at an average rate of 150.2 ± SD 13.4 m$^3$ sec$^{-1}$.

Although some sections of the lower River Shannon are important for coarse fishing, much of this stretch of river channel has been successfully developed, and is internationally renowned, for salmon angling. The diversion of water from the main river channel in 1929 had a profound impact on the physical nature and ecology of the river. Many areas of the river channel became dry, resulting in a significant and immediate loss of salmonid spawning habitat (Went 1970). Natural encroachment of bankside vegetation also occurred, and islands emerged in many areas and now permanently braid the channel. There is a long history of construction of instream features on salmon rivers in Europe, and prior to the impact of the hydroelectric works numerous pools had been developed on the lower River Shannon. These pools have been maintained, and many instream structures have been constructed to cater for the reduced flows. This work has generally been carried out on an ad hoc basis since the 1930s.

The survey site was typical of riffle sections of this lower section of the River Shannon. The channel was broken by a series of small islands, and the site was bounded to the north and the south by a series of small, artificially created falls (Fig. 1). The water depth ranged between 15 cm and 60 cm, with a substrate comprised mainly of pebbles and slightly larger rocks.

Fig. 1— a) maps of the River Shannon, (b) the lower River Shannon and (c) and the study site.
EELS (\textit{Anguilla anguilla} (L)) OF THE LOWER RIVER SHANNON

\section*{METHODS}

The site was electrofished on ten occasions between April 1996 and April 1997. On each sampling occasion a series of twenty-minute fishings were carried out, with eel as the only target species. Details of the number of fishings, water temperatures, conductivity and the total area fished were recorded. Although only single fishings were carried out, electrofishing is known to be an effective method of capturing eels at this location, and so relative densities (no. eels m\(^{-2}\) fished) of eels were calculated as an index of density. On capture the eels were anaesthetised, weighed to the nearest gram, individually bagged and numbered and transported back to the laboratory on ice to help preserve stomach contents. Eels were then frozen and stored at \(-15^\circ\text{C}\) for several months prior to further analysis. Following thawing the length of each eel was measured. Subsamples of eels representative of each sampling date were selected for dietary analysis. Stomachs were dissected out, percentage stomach fullness estimated by eye, and food items then identified to group level.

Saggital otoliths were removed from all eels and allowed to dry for at least a week before further processing. The otoliths were aged using two different methods. The first involved the burning and cracking of otoliths and was used on larger otoliths. Smaller otoliths were aged after they had been cleared in creosote. These methods had already been proven to be suitable for use on the lower River Shannon eels (Cullen and McCarthy 2003).

\section*{RESULTS}

A total of 1467 eels were captured over the study period, and an overview of the results for each of the ten occasions on which sampling took place is presented in Table 1. There was an apparent seasonality to the capture rate of the eels, with lower rates recorded during the winter months. This was confirmed by means of a partial correlation of capture rate with temperature, controlling for conductivity (correlation coefficient: 0.696, \(p = 0.037, n = 13\)).

The sizes of eels captured ranged from 76mm to 742mm, with an overall mean size of 200.5mm. However, the largest individual captured was of exceptional size in relation to the bulk of eels captured, with approximately 99% of the overall sample of eels captured less than 400mm length (Fig. 2). The weights of eels captured ranged from less than 1g to a maximum of 754g in the case of the largest eel captured, with 58% of the individuals caught less than 10g weight and 99% of the sample less than 100g. The overall relationship between length and weight was expressed by the regression \(\log \text{wt} = 3.176 + 6.228 \times \log \text{lt} \), \(R^2 = 0.96\). There were no apparent seasonal differences in the condition factors of the eels captured. Eels in the smallest length size category (<100mm), which were generally accepted to be those spending their first year in freshwater, were seen to be present in all months, but were less numerous in winter months. No apparent trend as to their time of immigration upstream to this region from estuarine waters was found.

A total of 1372 individuals were successfully aged. Freshwater age was calculated in all cases, i.e.

\begin{table}[!ht]
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\begin{tabular}{ccccccccc}
\hline
Water temperature (\degree C) & Conductivity (\mu S cm\(^{-1}\)) & No. of eels & Time fished (min) & Area fished (m\(^2\)) & Relative density (no. m\(^{-2}\)) & Capture rate (no. man-hr\(^{-1}\)) \\
\hline
04 April 1996 & 8 & 152 & 180 & 100 & 350 & 0.51 & 54.0 \\
10 May 1996 & 11 & 164 & 181 & 125 & 380 & 0.48 & 43.4 \\
19 June 1996 & 19 & 230 & 195 & 100 & 320 & 0.61 & 58.5 \\
25 July 1996 & 19 & 470 & 118 & 40 & 160 & 0.74 & 88.5 \\
03 Sept 1996 & 16 & 460 & 103 & 60 & 220 & 0.47 & 51.5 \\
08 Oct 1996 & 11 & 423 & 174 & 100 & 300 & 0.58 & 52.2 \\
11 Nov 1996 & 9 & 384 & 93 & 80 & 280 & 0.33 & 34.9 \\
19 Dec 1996 & 6.5 & 404 & 111 & 100 & 320 & 0.35 & 33.3 \\
27 Jan 1997 & 6 & 549 & 129 & 80 & 260 & 0.50 & 48.4 \\
17 April 1997 & 11.5 & 460 & 183 & 80 & 260 & 0.70 & 68.6 \\
\hline
Overall & 1467 & 865 & 2850 & & 0.51 & 50.9 \\
\hline
\end{tabular}
\caption{Details of the numbers of eels captured by electrofishing at the lower River Shannon site on ten dates between April 1996 and April 1997, together with information on water temperature, conductivity, areas fished and length of fishing times.}
\end{table}
0+ indicates an elver that has just arrived in freshwater. In the overall sample eel ages ranged from a minimum of 0+, to a maximum of 30+ in the case of the largest individual sampled, although the absolute age of this individual is somewhat doubtful due to difficulties in reading the outermost part of the otolith. The average age of the eels sampled was 8.2 years. The relationship between length and age was used in the calculation of a von Bertalanffy growth curve (Fig. 3).

As was the case with the mean lengths and weights of the eels, there was some variation in the mean age of elver capture in each of the ten samples analysed. Similarly, variation occurred in respect of the mean size of elver in each of the age groups throughout the sampling period. It had been hoped that it would be possible to analyse the seasonal changes in growth rates of the eels sampled. However, due to a number factors—the number of age groups present in each sample, the low number of eels in each of the age groups in each sample and the variable size range of eels at each age—it was felt that this analysis would not be possible.

Stomach contents from a subsample of 30 eels from each of the ten sampling dates were analysed. As can be seen in Fig. 4 there is a clear seasonal pattern to the feeding behaviour of the eels in terms of both mean percentage stomach fullness and the number of eel stomachs containing food items. With the exception of the sample from the month of July 96, when eels larger than 300mm were generally absent from the sample analysed, no overall differences in the length frequencies of eels whose stomach contents were examined were noted (Mann–Whitney U tests, p > 0.05). Similarly no overall differences were found between the length frequencies of the samples of eels whose stomach contents were examined and the monthly sample from which they originated (Mann–Whitney U tests, p > 0.05). Of the 120 eel stomachs examined from the months of May, June, July and September 1996, 94 contained prey remains, and of these only eleven contained remains that could not be positively identified.

The relative densities of eels at the lower River Shannon site during the current study were similar to values recorded during previous electrofishing surveys of the same region (McCarthy et al. 1999). These high relative densities are typical of the lower reaches of a river system and were shown to be significantly higher than those recorded further upstream in the Shannon system (Cullen 1999). Similar results have been recorded for many other European river systems (Aprahamian 1986; Feunteun et al. 1998). Another feature that is typical of high density, lower river eel populations is small eel size, and results similar to those recorded in the current study have also been recorded by many authors (Legault 1986; Naismith and Knights 1993; Lobon-Cervia et al. 1995; Feunteun et al. 1998). Indeed, previous studies of eels on the Shannon system have indicated that the lower River Shannon region produces predominantly male eels, which mature at a maximum of approximately 430mm (McCarthy et al. 1999; McCarthy and Cullen 2000a).

The results of the ageing studies in the present investigation indicated that the eels had a relatively slow growth rate. This is not atypical of a population that is dominated by male eels, and
these results agree with those of other studies of eels of temperate waters (Naismith and Knights 1993; McCarthy et al. 1999). The current study involved the comprehensive sampling, where possible, of all year classes present in the population. This is important in the study of growth rate of eels due to a number of reasons (Sinha and Jones 1967b; Tesch 1998). Irregularities occur in length at age data, with wide ranges on the sizes of eels in each age class and considerable overlap between age classes. The wide variation in eel growth throughout the species range is also the reason why growth models such as the von Bertalanffy growth curve, which is frequently used for other fish species, sometimes do not fit, as eels do not necessarily follow the conventional growth patterns of other fish species.

As eels are temperature dependent, populations in Northern European locations tend to become noticeably less active as water temperatures drop in the winter months, and they remain inconspicuous and relatively inactive until temperatures again rise in the spring (Tesch 1999). Water temperature is known to affect the efficiency of capture of fish by

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**Table 2—Summary of the dietary composition of the lower River Shannon electrofished eels examined during the months of May, June, July and September 1996. Data is presented both in terms of numbers of prey individuals identified (No.) and their frequencies of occurrence, i.e. no. of eels in which they occurred (Freq.).**

<table>
<thead>
<tr>
<th></th>
<th>May</th>
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<th>June</th>
<th></th>
<th>July</th>
<th></th>
<th>September</th>
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<tbody>
<tr>
<td>Hirudinea</td>
<td>1</td>
<td>1</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>1</td>
<td>–</td>
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<tr>
<td>Cladocera</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Isopoda</td>
<td>15</td>
<td>3</td>
<td>69</td>
<td>8</td>
<td>4</td>
<td>2</td>
<td>6</td>
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<tr>
<td>Amphipoda</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>–</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>5</td>
<td>4</td>
<td>37</td>
<td>8</td>
<td>52</td>
<td>8</td>
<td>26</td>
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<tr>
<td>Ephemeroptera</td>
<td>55</td>
<td>14</td>
<td>99</td>
<td>20</td>
<td>53</td>
<td>14</td>
<td>25</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>29</td>
<td>7</td>
<td>231</td>
<td>15</td>
<td>19</td>
<td>8</td>
<td>371</td>
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<tr>
<td>Odonata</td>
<td>4</td>
<td>3</td>
<td>–</td>
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<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Hemiptera</td>
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<td>3</td>
<td>2</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Diptera</td>
<td>3</td>
<td>2</td>
<td>9</td>
<td>5</td>
<td>7</td>
<td>6</td>
<td>76</td>
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<tr>
<td>Coleoptera</td>
<td>–</td>
<td>–</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
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<tr>
<td>Fish</td>
<td>3</td>
<td>3</td>
<td>–</td>
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<td>–</td>
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electrofishing. Because many fish are less active at colder temperatures they can remain hidden in burrows, crevices, etc., and thus are more difficult to catch by electrofishing (Zalewski and Cowx 1990). If the rate of capture recorded during the current study is taken as an index of eel activity, then by correlating water temperature against rate of capture while controlling for water conductivity, which is also known to affect the efficiency of electrofishing (Zalewski and Cowx 1990), it was possible to demonstrate this temperature influenced nature of the lower River Shannon eels’ activity.

Seasonality in the feeding behaviour of eels has also been documented elsewhere (Thomas 1962; Sinha and Jones 1975), and eels in temperate regions generally tend to cease feeding or feed to a lesser extent during the winter months (Tesch 1999). There was a definite seasonal pattern in the feeding behaviour of the lower River Shannon eels, and while some feeding did occur during the colder months of the year, the main feeding season ran from May to September. Similarly there was some evidence of seasonal differences in the composition of the diet. While some food items were only seen in the diet of these eels in the earlier months (e.g. fish), others (such as dipteran larvae) increased in importance later in the season. Eels are known for the diverse range of prey items that they ingest, making use of much of the aquatic fauna in the regions they inhabit, and it has also been noted that the composition of the diet can change seasonally, reflecting changes in the aquatic community (Tesch 1999). Coupled with the fact that eels are also known to stay within limited home ranges, especially during the feeding season (McGovern and McCarthy 1992; Tesch 1999), it is therefore likely that the diet of the lower River Shannon eels reflects composition of the available macroinvertebrate community at the study site and in the area surrounding the site. In general, the macroinvertebrates recorded from the food of the eels are not unusual for a riffle area. Indeed, in a review of the macroinvertebrate communities of the River Shannon, Bowman (1998) found that in the faster flowing reaches of the lower River Shannon the macroinvertebrate community is dominated by ephemeropterans and trichopterans.

In general, larger prey, such as fish, were absent from the diets of most of the lower River Shannon eels. As with many other fish species, the size of prey generally increases with that of the eel (Cairns 1941; Costa et al. 1992). Although during this study no overall trend was observed in respect of increases in prey size with eel size, it was clear that some of the larger prey items were only found in larger eels. Leech remains were only found in eels of length greater than 200mm, and larger prey items such as Odonata and fish were only found in eels greater than 300mm.

The impact of eels on other fish stocks, in particular salmonids, has long been the concern of salmon fishery managers. Although preliminary analysis by Mann and Blackburn (1991) suggested strong overlap in the diets of salmonids and eels, further analysis indicated distinct differences in the feeding behaviours of both groups that would minimise competitive impacts. They also concluded that as the eel population in the stream they surveyed consisted primarily of individuals less than 400mm length, piscivory on salmonids was not likely to be a problem. In a survey of a number of studies carried out in England (Frost 1946; Jones

<table>
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<th>Table 3 — A summary of the numerical composition of the diets of the lower River Shannon eels in each of four size categories.</th>
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<tr>
<td><strong>Size Category</strong></td>
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<td>No. eels</td>
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<tr>
<td>No. eels with prey</td>
</tr>
<tr>
<td>Hirudinea</td>
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<tr>
<td>Cladocera</td>
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<td>Isopoda</td>
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<td>Amphipoda</td>
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<td>Gastropoda</td>
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<td>Ephemeroptera</td>
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<td>Trichoptera</td>
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<tr>
<td>Odonata</td>
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<td>Hemiptera</td>
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<td>Diptera</td>
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<tr>
<td>Coleoptera</td>
</tr>
<tr>
<td>Fish</td>
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<tr>
<td><strong>Total</strong></td>
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and Evans 1960; Thomas 1962; Sinha and Jones 1967a) by Michel and Oberdorff (1995) the authors found that salmonophagous eels represented only 1% of the overall numbers examined. Bearing these facts in mind, and given that the lower River Shannon eel population is generally dominated by smaller male eels (McCarthy et al. 1999; McCarthy and Cullen 2000a), it is likely that piscivory among lower River Shannon eels is minimal. The fact that this area of the Shannon has historically been important as a commercial silver eel fishery yet remains an internationally renowned salmon fishery suggests that it is unlikely that the local eel population has had or will have a deleterious impact on the salmonids of the area.

The widespread collapse of European eel Anguilla anguilla (L.) stocks is a matter of great concern (Moriarty and Dekker 1997; ICES 2005), and there is now increasing need for greater knowledge of the population biology and general ecology of all populations of European eel throughout its range (W. Dekker, pers. comm.), in particular if conservation strategies are to be successfully implemented. As this study has indicated, there is considerable knowledge available on lake populations of eels, and to a lesser degree on stream populations, in particular the mature downstream migrating proportion of stream populations. There are, however, few studies on the resident populations of some of Europe’s large rivers. This study has highlighted the presence of a dense population of eels in the lower reaches of one such large river, the River Shannon. This population is of importance not only for the numbers of mature migrating silver eels it can potentially contribute to the spawning stock but also because it has been recognised as a good source of fingerlings and bootlace eels suitable for restocking the lakes of the Shannon system (McCarthy et al. 1999; McCarthy and Cullen 2000b). The approach taken in this study, of analysing many aspects of the eels’ biology and ecology over an annual cycle, and other long-term approaches to the study of eels should be encouraged. As was shown there was considerable variation in many of the factors information recorded in each of the individual samples (sizes and ages of eel, dietary composition, rate of capture).

However when taken as a whole the information gathered from all samples gives a clearer picture of the biology and ecology of the population studied. The longevity of European eels and the seasonality of their behaviour, in particular in populations inhabiting the cooler waters of northern Europe, means that in order to truly understand the biology of the species and maximise the outcome of conservation strategies, long-term and integrated studies are necessary.

ACKNOWLEDGEMENTS

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