Environment Agency

Evidence

Developing Life Tables for English and Welsh Eel Stocks

Report – SC060028/R

The Environment Agency is the leading public body protecting and improving the environment in England.

It's our job to make sure that air, land and water are looked after by everyone in today's society, so that tomorrow's generations inherit a cleaner, healthier world.

Our work includes tackling flooding and pollution incidents, reducing industry's impacts on the environment, cleaning up rivers, coastal waters and contaminated land, and improving wildlife habitats.

This report is the result of research commissioned and funded by the Environment Agency.

Published by:
Environment Agency, Horizon House, Deanery Road, Bristol, BS1 5AH
www.environment-agency.gov.uk

ISBN: 978-1-84911-303-8

© Environment Agency – June 2013

All rights reserved. This document may be reproduced with prior permission of the Environment Agency.

The views and statements expressed in this report are those of the author alone. The views or statements expressed in this publication do not necessarily represent the views of the Environment Agency and the Environment Agency cannot accept any responsibility for such views or statements.

Further copies of this report are available from our publications catalogue: http://publications.environment-agency.gov.uk or our National Customer Contact Centre: T: 08708 506506
E: enquiries@environment-agency.gov.uk.

Author(s):
Walker, A.M., Apostolaki, P. & Pawson, M.

Dissemination Status:
Publicly available

Research Contractor:
Cefas
Pakefield Road
Lowestoft
Suffolk
NR33 0HT

Environment Agency's Project Manager:
Miran Aprahamian

Project Number:
SC060028

Evidence at the Environment Agency

Evidence underpins the work of the Environment Agency. It provides an up-to-date understanding of the world about us, helps us to develop tools and techniques to monitor and manage our environment as efficiently and effectively as possible. It also helps us to understand how the environment is changing and to identify what the future pressures may be.

The work of the Environment Agency's Evidence Directorate is a key ingredient in the partnership between research, guidance and operations that enables the Environment Agency to protect and restore our environment.

This report was produced by the Scientific and Evidence Services team within Evidence. The team focuses on four main areas of activity:

- **Setting the agenda**, by providing the evidence for decisions;
- **Maintaining scientific credibility**, by ensuring that our programmes and projects are fit for purpose and executed according to international standards;
- **Carrying out research**, either by contracting it out to research organisations and consultancies or by doing it ourselves;
- **Delivering information, advice, tools and techniques**, by making appropriate products available.

Miranda Kavanagh

Director of Evidence

Executive summary

The European eel, *Anguilla anguilla*, is widely distributed throughout European estuarine and inland waters. However, estimates at the glass eel stage indicate that recruitment across Europe has fallen to below five per cent of historic levels. Since 2000, The International Council for the Exploration of the Seas (ICES) has advised that the stock is outside safe biological limits and that current fisheries are not sustainable.

The European Commission has initiated an Eel Recovery Plan to return the European eel stock to sustainable levels, with each Member State required to establish national Eel Management Plans (EMPs). These plans aim to achieve an escapement of silver eel to the spawning population that equals or exceeds 40 per cent of the potential biomass that would be produced under conditions with no anthropogenic disturbance due to fishing, water quality or barriers to migration.

The aim of each EMP is to describe the nature of the eel population and fishery within a defined area, to assess whether the stock is meeting its 40 per cent escapement target, and to present management actions that will ensure the long-term viability of the eel population.

In England and Wales, the Environment Agency is responsible for the management of eel stocks and associated fisheries in inland waters and in tidal waters to a distance of six nautical miles. As the eel management target has been defined in terms of silver eel weight, the most direct compliance assessment would be through the capture and weighing of emigrating silver eels. However, in the absence of widespread direct monitoring of silver eel escapement in England and Wales, a habitat-based modelling assessment approach relating information on (routinely monitored) yellow eel populations to silver eel production and escapement is required by the Environment Agency.

Currently, the Environment Agency is focusing on reducing fishing pressure, improving access and habitat quality, reducing the impacts of entrainment, and stocking, as measures to increase silver eel escapement. Any forward-looking assessment model therefore needs to be able to incorporate such anthropogenic impacts on the dynamics of the eel population, and to allow the user to simulate their removal or amelioration so as to compare the net benefits of various management measures. An effective eel life history model must enable biological reference targets to be set and compliance with these targets to be assessed.

The overall objective of this project, therefore, was to provide the Environment Agency with a fully developed and parameterised eel life-history model that can be applied to stocks in English and Welsh rivers in order to:

- establish the reference level for silver eel escapement, according to the management target required by the European Eel Recovery Plan;
- estimate present day and future trends in silver eel escapement;
- establish intermediate (or proxy) targets for other life stages (glass eel, yellow eel) that will enable the management target to be met;
- guide the data collection, monitoring and enforcement of regulations required to estimate whether compliance with the target has been achieved.

The level of complexity that characterises the life cycle of eel populations makes simulating its dynamics particularly challenging. This report reviews the model options that were available at the start of the project, building on work undertaken as part of the 2007 European Study Leading to Informed Management of Eels (Slime) programme,

before describing the development of the proposed framework based on what scientific understanding there is of the eel life cycle and how to accommodate various scenarios in long term modelling activities.

The new model, SMEP II, is a software package developed to model the dynamics and exploitation of eel populations, based on the model (SMEP) originally developed by Bark, Knights, Kirkwood, El-Hosaini and Williams.

The model works on the scale of a river basin and consists of three main components:

- A model that simulates both the biological characteristics of the eel population and a number of potential anthropogenic influences on that population.
- A GIS tool that helps the user determine the spatial structure that they want to use for their calculations and prepare the input files for the population dynamics model to run.
- A statistical model that is used to estimate some of the parameters of the population dynamics model.

The final chapter of the report acts as a comprehensive user guide for the SMEP II model, and illustrates the potential application of SMEP II to address the requirements of the Environment Agency in assessing and managing eel stocks.

Recommendations for areas of further research are also given, to help tackle gaps in our understanding of the life history and behaviour of eels that limit our ability to simulate eel production, and holes in available data on which to test and apply SMEP II.

Acknowledgements

This project was funded by the Environment Agency. Thanks are due to the Environment Agency and the Department for Environment Food and Rural Affairs (Defra) for providing access to their data (Defra data were collected by Kings College London under contract SFO236), and to the Environment Agency project team lead by Miran Aprahamian for their contributions to the development of this project and report. In addition to the authors listed above, a number of staff from the Centre for Environment, Fisheries and Aquaculture Science (Cefas) contributed to the project and their contributions are acknowledged here: Michael Godard for field sampling and data processing, Stephan Manley for data entry, Janette Lee and David Stephens for GIS programming, and David Maxwell and Lisa Readdy for statistical analyses.

The conclusions and views expressed are those of the authors and not necessarily those of Cefas or the Environment Agency.

Contents

1	**Introduction**	**1**
2	**Selection of model framework**	**3**
2.1	Eel models	3
2.2	Model features for consideration	4
2.3	Review of modelling approaches	4
2.4	Discussion of models used in SLIME	4
2.5	Other models not considered by SLIME	7
2.6	Discussion	8
3	**Development of the model framework**	**10**
3.1	SMEP II - Model description	10
3.2	User inputs to model framework	22
4	**Description of processes and selection of parameters**	**24**
4.1	Introduction	24
4.2	Growth	24
4.3	Gender differentiation	31
4.4	Mortality rates	34
4.5	Maturation (silvering)	37
4.6	Movement of eels throughout a basin	38
4.7	Quality of habitats and carrying capacity or productive potential	41
4.8	Quantitative estimates of silver eel production	42
4.9	Recruitment /settlement	43
5	**Application of the model (user guide)**	**45**
5.1	Parameterising and running the model	45
5.2	Model outputs	63
5.3	Example applications	63
6	**Recommendations for further research and development**	**80**
6.1	Introduction	80
6.2	Knowledge and understanding of eel life history processes	80
6.3	Knowledge and understanding of eel behaviour	82
6.4	Model testing	83
6.5	Model application	83
References		**85**

Table 1. Sexual differentiation in *Anguilla anguilla*, maximum lengths of undifferentiated eels and minimum lengths of sexually differentiated eels sampled from rivers in England and Wales during the Defra CTG0102 contract. 31

Figure 3.1. A possible branching configuration and selection of reaches when considering eel movements in a river 15
Figure 3.2. Types of curves that the model can use to describe the proportion of differentiating eels that become females at different levels of relative density. 16
Left panel: Ogive type I, Right panel: Ogive type II. The numbers in the captions correspond to different values for the model parameter (ρ for Type I curves and λ for Type II curves) that determines the slope of the curves.16
Figure 3.3. Weibull curves for three different values of the parameter ν . If density effects are taken into account, and ν_{min}=0.1 while ν_{max}=0.3, the curve that corresponds to ν =0.2 would give the values of M when the biomass of the relevant group (i.e. undifferentiated) was equal to 50 per cent of its reference biomass.19
Figure 3.4. Functions of natural mortality-at-length, and corresponding survival rates, for extreme mortality 'gamma' values. The two lines of coloured symbols for natural mortality define the range of values of natural mortality that are allowed for each length. Similarly, the two solid lines define the maximum and minimum values of mortality and survival for each eel length that SMEP II applies, depending on the levels of density of eels relative to the Critical Density (that is, MaxBDensity in the Parameters.csv file: see Chapter 5). 20
Figure 3.5. Single logistic functions for maturation at length for both males and females. 21
Figure 4.6. Fit of different growth models to length at age data from four rivers. The red line corresponds to the linear model. 26
Figure 4.7. Length-weight distributions for yellow and silver eel from English and Welsh rivers. 30
Figure 5.1. Example configuration of the First_File.csv. 47
Figure 5.2. Example configuration of the Parameters.csv file. Note that the process parameters are coloured here (the .csv file format does not support coloured fonts) to indicate those that the user could consider varying (green), those that are unlikely to vary except if robust local eel data are available (amber), and those that we strongly advise against changing (red). 50
Figure 5.3. Example river network illustrating the component included in the model simulation (blue line) and the reach labels (1-10). 52
Figure 5.4. Example configurations of the ReachDefinition.csv and DistanceFromSea.csv files, derived from the river network illustrated in Figure 5.3. 53
Figure 5.5. Example configuration of the Barrier Details table created in the RiverReach tool where the user can specify the location of each structure and the proportion of potentially moving eels that are able to move upstream or downstream. 53
Figure 5.6. Example configuration of the ReachPositioning.csv file, derived from the river network illustrated in Figure 5.3. The diagonal values are shown in red font, and the barrier proportions are shown in blue font (see below). 54
Figure 5.7. Example configuration of the EnvHabScores.csv file for a river network with 10 reaches, simulating 15 years of eel production. Cell values are the proportion of the Maximum Biomass Density of eels that the reach can sustain (0-1). Reaches 4 and 7 are of less than ideal habitat quality in year 1, but habitat quality is improved and attains the ideal state in years 9 and 4, respectively. 55
Figure 5.8. Densities of eel at survey sites along the length of the River Blyth, Northumberland, sampled by eel-specific electrofishing by Bark, Knights and Williams (unpublished Defra data). The red arrow indicates the location of a substantial weir that appears to affect the distribution of eels. The purple lines and numbers indicate the two putative zones of different eel density. 58
Figure 5.9. Densities of eel at survey sites along the length of the River Ellen, Northumberland, sampled by eel-specific electrofishing by Bark, Knights and Williams (unpublished Defra data). The red arrows indicate the location of substantial weirs that appear to affect the distribution of eels. The purple lines and numbers indicate the putative eel density zones. 58
Figure 5.10. Example configuration of the TotalCatchByStage.csv file for a river network, simulating six years of fishing exploitation. Glass eel and yellow eel fishing occurs throughout the period but the silver eel fishing ceases after year 2. 61
Figure 5.11. Example of the FishingPractices.csv file configured to represent the mortality associated with a turbine facility located at the lower end of Reach 3. The turbine causes a mortality of 20 per cent on eels above 300mm length in the third season (autumn), but this is reduced to zero after year five. 62
Figure 5.12. Example of the Stocking.csv file configured to represent the spring-time stocking of 120,000 glass eel (mean length 80mm) into Reach 6 in year five, with further stockings of 60,000 each in years six and seven. 62
Figure 5.13. Schematic representation of the river network GIS map used in the example applications of SMEP II. The riverline is shown in green, the boundaries between the 15 reaches are shown as blue dashed lines, the most downstream location is shown as DS, the survey sites are shown as red crosses, the silver eel fishery in Reach 3 is shown as SE, and the turbine between Reaches 8 and 9 is shown as T. 64
Figure 5.14. Extracts from the ReachDefinitions.csv and DistanceFromSea.csv input files used in the example applications of SMEP II for the river basin shown in Figure 5.13. 65
Figure 5.15. Extract from the First_File.csv input file used in the example applications of SMEP II for the river basin shown in Figure 5.13. 66
Figure 5.16. Extract from the Parameters.csv input file used in the example applications of SMEP II for the river basin shown in Figure 5.13. 67
Figure 5.17. Annual production of silver eel (kg: blue line) of the study river basin under equilibrium conditions, with annual recruitment varying from 500,000 to 5 million elvers. The variation in silver eel biomass between years as a percentage of the maximum production is presented by the red line. 67
Figure 5.18. Numbers of male (red line) and female (blue) silver eels produced from varying levels of recruitment, and the resultant % females amongst the emigrants (green). Note that silver eel production is unstable at recruitment above about 3 million, but the data are shown here for comparison with Figure 5.17. 68
Figure 5.19. The development of the yellow eel population towards equilibrium, at recruitment of 3 million elvers per annum. The average whole-river density per 100m^2 is shown by the blue line, and the average whole-river biomass per 100m^2 is shown by the red line. 69
Figure 5.20. The annual silver eel production in numbers (blue line) and biomass (kg: red line) from the yellow eel population as it develops towards equilibrium, at recruitment of 3 million elvers per annum. 69

Figure 5.21. Dispersal of yellow eels throughout the 15 reaches of the river basin, represented by the first year when eel densities achieve at least 1 eel per 100m^2 in each reach. 70
Figure 5.22. Extract from the UserInputLFperReach.csv file used to illustrate model application to estimate present silver eel production, and project future production under various management scenarios. Note the extract is truncated at 29 length classes for brevity but the file has 100 length classes (0-1000mm in 10mm length bins). 71
Figure 5.23. Projected trend in silver eel escapement (numbers: blue line) from the baseline condition with yellow and silver eel fisheries and turbine mortality, and trend in recruits (red line) as a proportion of the maximum stable recruitment level. 75
Figure 5.24. Projected trend in silver eel production (biomass: blue line) from the baseline condition with yellow and silver eel fisheries and turbine mortality. 75
Figure 5.25. Projected trend in silver eel production (numbers) over 45 years with recruitment increasing from years 15 to 45 (as Figure 5.23). The baseline production with no control of fishing or turbine mortalities is shown by the dark blue line. The effects of closing the yellow or silver eel fishery, removing the turbine mortality or removing all mortalities from year 4 onwards are shown by the red, green, purple and pale blue lines, respectively. 76
Figure 5.26. Projected trend in silver eel production (biomass, kg) over 45 years with recruitment increasing from years 15 to 45 (as Figure 5.23). The baseline production with no control of fishing or turbine mortalities is shown by the dark blue line. The effects of closing the yellow or silver eel fishery, removing the turbine mortality or removing all mortalities from year 4 onwards are shown by the red, green, purple and pale blue lines, respectively. 76
Figure 5.27. Projected trend in silver eel production (numbers) over 45 years with recruitment increasing from years 15 to 45 (as Figure 5.23). The baseline production with no control of fishing or turbine mortalities is shown by the blue line. The effects of stocking in Reach 15 in years 5, 7, 9, 11 and 13 while continuing the fishing and turbine mortalities is shown as the red lie, compared to removing all mortalities from year 4 onwards (green) and stocking Reach 15 in each of these years (purple). 77
Figure 5.28. Projected trend in silver eel production (biomass, kg) over 45 years with recruitment increasing from years 15 to 45 (as Figure 5.23). The baseline production with no control of fishing or turbine mortalities is shown by the blue line. The effects of stocking in Reach 15 in years 5, 7, 9, 11 and 13 while continuing the fishing and turbine mortalities is shown as the red lie, compared to removing all mortalities from year 4 onwards (green) and stocking Reach 15 in each of these years (purple). 78

1 Introduction

The European eel, *Anguilla anguilla*, is widely distributed throughout European estuarine and inland waters. Estimates at the glass eel stage indicate that recruitment across Europe has fallen to below five per cent of historic levels. Since 2000, The International Council for the Exploration of the Seas (ICES) has advised that the stock is outside safe biological limits and that current fisheries are not sustainable (ICES, 2001).

The European Commission has initiated an Eel Recovery Plan (Council Regulation No 1100/2007, hereafter the Regulation) to return the European eel stock to sustainable levels of adult abundance and glass eel recruitment. Each Member State is required to establish national Eel Management Plans (EMPs). These plans aim to achieve an escapement of silver eel to the spawning population that equals or exceeds 40 per cent of the potential biomass that would be produced under conditions with no anthropogenic disturbance due to fishing, water quality or barriers to migration. Each Member State is required to:

- set management targets based on the potential silver eel production under conditions of no anthropogenic mortality and high (pre-1980) levels of recruitment;
- estimate the present day silver eel escapement against this target;
- implement management actions necessary to achieve or maintain compliance with this target;
- collect data to support steps 1 to 3 above, and to demonstrate whether compliance will be achieved in the future.

In England and Wales, eel legislation and policy is determined by the Governments, through the Department for Environment Food and Rural Affairs (Defra) for England, and the Welsh Assembly Government for Wales. In both countries, the Environment Agency is responsible for the management of eel stocks and associated fisheries in inland waters and in tidal waters to a distance of six nautical miles. In accordance with the recommendations set out in the Regulation, River Basin Districts (RBDs) developed for the Water Framework Directive (WFD) have been set as management units for England and Wales.

The aim of each EMP is to describe the nature of the eel population and fishery in the RBD, to assess whether the stock is meeting its 40 per cent escapement target, and to present management actions that will ensure the long-term viability of the eel population. Article 2.5 of the Regulation sets out three approaches to assessing compliance with the target. These are:

- use of data collected in the most appropriate period prior to 1980, provided these are available in sufficient quantity and quality;
- habitat-based assessment of potential eel production, in the absence of anthropogenic mortality factors;
- with reference to the ecology and hydrography of similar river systems.

As the eel management target has been defined in terms of silver eel weight, the most direct compliance assessment would be through the capture and weighing of emigrating silver eels. However, few silver eel fisheries operate in England and Wales, and the installation and operation of new traps is restricted practically and financially. In contrast, yellow eels are routinely monitored by the Environment Agency throughout

the RBDs, either during multi-species or eel-specific electric fishing surveys. In the absence of widespread direct monitoring of silver eel escapement, a habitat-based modelling assessment approach (combining the second and third of the above approaches) relating the information on yellow eel populations to silver eel production and escapement is required by the Environment Agency.

There are a number of options to increase silver eel escapement, but at present the Environment Agency has focused on the potential across England and Wales for reductions in fishing pressure, improving access and habitat quality, reducing the impacts of entrainment, and stocking, with the interplay of options varying between rivers and basins depending on local priorities and opportunities. It is necessary, therefore, for any forward-projecting assessment model to incorporate such anthropogenic impacts on the dynamics of the eel population, and to allow the user to simulate their removal or amelioration so as to compare the net benefits of various management measures.

Thus, the Environment Agency requires an eel life history model appropriate to the assessment and management of eel stock status in rivers throughout England and Wales, with which specifically to be able to set biological reference targets, assess compliance with these targets and evaluate management scenarios for the conservation of eel populations and sustainable management of associated fisheries. In addition, the Environment Agency requires definitions of monitoring schemes that will provide data to allow compliance and management measures to be assessed.

The overall objective of this project, therefore, is to provide the Environment Agency with a fully developed and parameterised eel life-history model that can be applied to stocks in English and Welsh rivers in order to:

- establish the reference level for silver eel escapement, according to the management target required by the European Eel Recovery Plan;
- estimate present day and future trends in silver eel escapement;
- establish intermediate (or proxy) targets for other life stages (glass eel, yellow eel) that will enable the management target to be met;
- guide the data collection, monitoring and enforcement of regulations required to estimate whether compliance with the target has been achieved.

To these Cefas would add:

- facilitate the cost-benefit analysis of management measures required to achieve compliance.

In this report, we describe the work undertaken to achieve this objective. The report is split into two main parts. In part one (Chapters 1 to 4), we review the model options that were available at the start of the project and explain the choice of a particular model framework. We then go on to describe the framework and the testing and developments undertaken during this project, and review the scientific knowledge base for the modelling of eel life history processes and the selection of process parameter values appropriate to eels in England and Wales. In part two (Chapters 5 and 6), we describe the application of the model framework in addressing the Environment Agency's requirements as set out above, and summarise topics that will benefit from further research and development. Chapter 5 includes guides on data requirements, running the model, and interpreting and using the results, and provides examples illustrating model application to selected river basins. The report concludes with a list of the references cited throughout. A separate annex document provides the detailed user guide for the Arc-GIS tool developed within the project.

2 Selection of model framework

This report is intended to summarise the state of play concerning eel population models and their development, as appropriate to meet the needs of the Environment Agency. This report is based on a review in 2007 of the models presented to the European Study Leading to Informed Management of Eels (SLIME) programme (Dekker *et al*., 2006), and other eel models not considered under SLIME, including those developed for other *Anguilla* spp. In each case, the models are considered in relation to the features required by the Environment Agency.

2.1 Eel models

The level of complexity that characterises the life cycle of eel populations makes simulating its dynamics particularly challenging. Studies have already focused on the development of population dynamics models for several eel species including the American eel (*Anguilla rostrata*), shortfin eel (*A. australis*) and longfin eel (*A. dieffenbachii*), and European eel (*A. anguilla*). The SLIME programme (Dekker *et al*., 2006) reviewed developments in quantitative modelling of European eel populations and tested different models in light of the management target proposed by the European Commission (note that the regulation was not implemented until late 2007). Six models were considered:

- GEMAC – Glass Eel Model to Assess Compliance (Beaulaton and Briand, 2007), France;
- LVPA – Length-based Virtual Population Analysis (Dekker in Dekker *et al*., 2006), The Netherlands;
- DemCam – Demographic model of Camargue eel (Bevacqua *et al*., 2007), Italy;
- SWAM – Swedish Analytical Models (Åström in Dekker *et al*., 2006), Sweden;
- SMEP – Scenario-based Model of Eel Populations (Aprahamian *et al*., 2007), UK;
- GlobAng – Global watershed model of Anguilla (Lambert and Rochard, 2007), France.

These models vary in approach from the life-history stage-specific (glass eel: GEMAC), through classical fishery-related length-based Virtual Population Analysis (LVPA), to spatially distributed demographic models, either applied at the gross scale of lagoons (DemCam) or Swedish coastal waters (SWAM), or specifically at catchments or tributaries (SMEP, GlobAng).

The research undertaken in SLIME constituted a good basis for deciding on the appropriate structure and characteristics of the model required by the Environment Agency. Below we examine the advantages and weaknesses of each of the models used in SLIME in an attempt to incorporate the most beneficial features of existing models into a single one to create a more complete, effective, modelling framework. This framework should encapsulate the complex life history of the European eel in freshwater and estuaries, and simulate the various types of anthropogenic impact in addition to natural mortality. The model should also be capable of being used to inform

management processes, enable calculation of reference and target levels, and assess compliance with them.

2.2 Model features for consideration

Age-structured (and less frequently length-structured) models are the type of analytical population models that researchers use to simulate the dynamics of marine species when they need to make their simulations more realistic. However, most of those models are not able to adequately describe the complexity in the eel life cycle and would need to be modified to handle that complexity and the paucity of information regarding eel life history processes. The specific issues related to eel dynamics that need to be considered in the development of the model are:

- growth
- sex determination
- mortality
- silvering
- dispersal
- habitat quality
- river topography
- anthropogenic impacts.

The literature review in section 3.3 provides a detailed explanation of each of these issues.

2.3 Review of modelling approaches

The models considered in SLIME were specifically developed to simulate the dynamics of European eel and address questions related to its status and management. Thus, their approaches could be highly relevant to our research. Below, we discuss the main features of those models and the processes they have chosen to simulate in order to decide on concepts that we can borrow from those studies and identify major gaps in model formulation.

2.4 Discussion of models used in SLIME

The models used in SLIME are discussed in two sections. The first describes three models that we feel have some interesting features but do not address many of the issues or features we need to consider within model development. Those models are LVPA, SWAM and GEMAC. The second section presents the three models that appear to be more relevant to our needs and can be used as a starting point for the development of the modelling framework (use of concepts or actual formulae). These models are the DemCam, GlobAng and SMEP.

2.4.1 SLIME - Models not addressing important issues or processes

LVPA (Dekker in Dekker *et al*., 2006) is a length-based virtual population analysis (VPA) that requires catch-at-length data to back-calculate the population of eels in the previous year. Although a length structured model seems appropriate for the simulation of eels, the methodology and the data requirements of LVPA do not allow for much flexibility in the analysis. For example, catch-at-length data are limited in the UK and are not available for areas where there is no fishing for eels. Further, the LVPA method assumes that fishing is an important component of the total mortality of eels, and focuses on understanding the effects of fishing. However, there are many other factors that could change the status of eel populations and could be equally or more important than fishing across England and Wales. Also, the model does not allow for density-, or sex-dependent processes which, as mentioned above, could play an important role in eel dynamics. These features do not fit particularly well with our requirements for a model that simulates different anthropogenic impacts and the dynamics of eels in different habitats, and that can be used for scenario testing.

The conceptual thinking behind the development of SWAM (Åström in Dekker *et al*., 2006) has many similarities with the model features and the management issues considered in this project. However, a considerable number of simplifications were made in the development of the mathematical model and the final product does not model the possible effect of sex, length or density on processes such as growth. Further, the majority of the different implementations of the model give predictions under equilibrium conditions instead of following the annual development of each cohort. However, the analysis does propose potential formulae for simulation of the number of silver eels of each sex.

GEMAC (Beaulaton and Briand, 2007) models the life of eels from the beginning of their continental life phase (glass eel) to pigmentation (recruitment to elvers). The model relates temperature and salinity levels to pigmentation time and uses a fine temporal scale for the calculations. Processes such as migration, settlement, and mortality due to fishing are also modelled. The model is spatially disaggregated, a feature that could be very useful when different types of habitat are considered, and facilitates simulation of eel movements. The theoretical framework also includes formulae that describe the efficiency of different fishing gears and could be useful in the development of our modelling framework. However, the model is restricted to the first stage of the continental phase of the life cycle and is not sufficient, in isolation, to meet our requirements.

2.4.2 SLIME – Models as a starting point for developing the framework

The DemCam (Bevacqua *et al*., 2007) model is a stage- and sex-structured population model which explicitly accounts for differentiation in eel growth. The model uses probabilities to describe the length of eels of a given age, which is a concept that it is expected to be important for the description of eel dynamics. The model simulates the continental phase of the eel life cycle (undifferentiated, yellow males, yellow females, silver males or silver females) and uses a stock-recruitment (S-R) function to relate glass eels to elvers. The use of S-R functions such as this is very common in the assessment of fish stocks. In our case, one of the factors that will determine the starting point for the calculations is whether information (such as abundance indices) is available for glass eels or elvers.

DemCam models sex differentiation as a function of size and population density, while maturation is assumed to be length dependent. The model also calculates the effects

of fisheries using different types of gears. The model can be fitted to catch or catch per unit effort (CPUE) data, but the results are given as point estimates (that is, no estimates of uncertainty). Fitting the model to catch and CPUE data can be useful when good fishery-dependent information is available. However, the model simulates the dynamics of eels in a single area and does not explicitly account for the effects of habitat quality in model predictions.

GlobAng (Lambert and Rochard, 2007) is an age-structured model that simulates the dynamics of undifferentiated, female yellow and male yellow eels and calculates the number of eels that reach the silver stage. The model requires recruitment time series and can calculate the population structure and size under equilibrium and non-equilibrium conditions. It uses a time step of one week, which is much smaller than the time step used in most other models considered in SLIME, although GEMAC uses one day for some processes. Such a fine temporal scale could be important for the simulation of processes such as dispersal and settlement, but it increases the processing time. The model explicitly accounts for area-specific saturation and uses saturation levels to determine the proportion of differentiated eels that become males or females and calculate changes in natural mortality. The age at sex differentiation and maturity, however, are modelled independent of density. Impacts such as fishing or barriers to migration are simulated in the model by increasing the mortality rates (fishing) and reducing the appropriate migration rates (barriers). The model does not simulate the growth of eels (length at age, for example) and processes dependent on size rather than age cannot be considered.

A feature that distinguishes this model from the others is its spatial structure. The model simulates the topography of a river (allowing the user to split the river tree into longitudinally homogenous reaches of constant length) and uses formulae that take into account saturation levels in each part of the river to determine the dispersal of eels. In the examples considered for SLIME, the model could split the area of a river into more than 500 compartments. However, such fine spatial scale in combination with a fine temporal scale affects the processing time of the model and causes problems when the model is fitted to data. Another problem that arises concerns the number of estimated parameters, which can increase very quickly at finer spatial scales. Thus, calibration of the model can become problematic. This is one of the reasons why Lambert and Rochard (2007) chose to follow specific steps in their simulation testing. As part of that testing they performed all necessary simulations and systematically compared simulated results with the pattern (selected) in order to determine which combinations of parameter values are compatible with it. This experimental approach to simulation allows the identification of the factors that have an effect and those that have no effect under a given set of assumptions. This exploratory approach is a very good starting point in understanding the behaviour of a model and can be useful for our analysis, but more tests will be needed for a complete model validation.

SMEP (Aprahamian *et al*., 2007) is an age-, length-, and sex-structured model that simulates the freshwater phase of the eel life cycle. The conceptual framework for SMEP shares many similarities with that of GlobAng. Both models use area specific saturation levels to describe the effects of density on processes such as sex differentiation, movement, mortality and growth (only SMEP). SMEP uses a spatially disaggregated approach but, contrary to GlobAng, it assumes that the different reaches in a catchment form a single straight line (that is, no river tree). However, unlike GlobAng, the size of each reach simulated within SMEP can differ in length and width. The time step used for the calculations (three months) is greater than that used in GlobAng (one week). Both time steps are smaller than the annual time step that is often used in population dynamics models. Whether a three-month step is adequate for the simulation of eel dynamics depends on the temporal scale of the processes we want to simulate, and on how important it is to increase the realism in the simulation of those processes. The model needs an annual recruitment series for all years for which

the simulation is run. That series can be in actual or relative numbers. In the latter case, the model can use estimates of the proportion of females for a given year and reach to estimate the previous recruitment in numbers that will result in the observed proportion of females. Population structure under equilibrium and non-equilibrium conditions can be modelled.

One of the main differences between SMEP and GlobAng is that SMEP explicitly models the growth (such as length) of eels and accounts for length dependence in the simulation of eel dynamics.

In December 2006, we approached those scientists who had presented models at SLIME (June 2006) to find out whether they had further developed and/or applied their models. There had been no further developments in the concepts of any of the models in the six months since SLIME. However, an assessment approach based on length structure analysis to evaluate local eel stock status (ELSA) was developed by Patrick Lambert, and was presented to the ICES Theme Session in September 2006, though not published in the proceedings.

2.5 Other models not considered by SLIME

Models which were not considered under SLIME and are of interest include the Reference Condition Model (RCM) (Aprahamian *et al*., 2007) and models developed to simulate the dynamics of eels in New Zealand (Francis and Jellyman, 1999) and North America (Reid, 2001).

The RCM is an attempt to provide estimates of eel density in a river using a simple empirical approach. The model is based on the assumption that the density of eel declines exponentially with increasing distance from the tidal limit, and therefore that we can assess yellow eel stock status by comparing the observed instantaneous rate of density decline with that expected according to the model relationship. The model uses information on the rate of decline of eel density with distance from tidal influence that is available for several catchments in England and Wales and has been used by the Environment Agency to inform the development of EMPs. The simplicity of the model makes it easy to use but also limits its potential since, for example, the model cannot be used to predict silver eel escapement or to explore the significance of different processes for the effectiveness of management actions. Note that the ICES evaluators of UK EMPs (in providing advice to the European Commission, Report of ICES Secretariat, November 2009) rejected the proposed use of the RCM because it does not provide a measure or estimate of silver eel escapement biomass.

The model developed by Francis and Jellyman (1999) to investigate whether mean size can be an effective indicator of the effects of exploitation on an eel population is an age-, length- and sex-structured model that simulates the continental phase of the life cycle of New Zealand shortfin and longfin eels. The model simulates many important processes such as maturation, growth and mortality, but does not model the pigmentation process (transformation of glass eel to elver), and the sex ratio is fixed. The model uses stochastic recruitment, and describes the length of eels at a given age according to a length distribution series. It does not allow for density dependence in the processes it simulates. Francis and Jellyman did not fit the model to data in their study (for example no optimisation routines and so on), but used sensitivity analysis to identify the parameters that were most influential. The generality of the model with regard to simulation of biological processes is relatively high. However, the model is not spatially disaggregated and as a result, cannot simulate the movement of eels. The model has recently been extended to include optimisation routines that allow the user to fit the model to observations (E. Graynoth, pers. comm.), but the source code is part of a commercial product and not freely available.

The Great Lakes Fishery Commission (GLFC) attempted to develop a life-history-based population dynamics model of American eel in order to identify critical data gaps and research priorities, and to assess potential measures to mitigate for stock decline (Reid, 2001). The model used a Beverton-Holt S-R function to simulate all life history transitions, with stage abundance predicted according to stage production and habitat capacity parameters. Life history transitions are:

Eggs → leptocephali → glass eels → elvers → undifferentiated yellow eels → differentiated yellow eels → silver eels → eggs.

Density-dependence is applied at all stages except silver eel production. The intention was to parameterise the model with data describing habitat capacity, stage-specific fishing mortality, stage-to-stage production (S/R function), mortality associated with habitat destruction and hydroelectric dams, and natural mortality of silver eel during oceanic migration. However, such data are sparse for the American eel, and it became apparent early in the model development that there were contradictions in almost every quantitative aspect where data existed. Sensitivity analyses of parameters were conducted by varying the onset of maturation (early or late), yellow eel habitat carrying capacity (fixed or variable) and leptocephali/glass eel production (fixed or variable), calculating silver eel and egg production over 1000 trials, and comparing the rank correlation of parameter values with the results.

The model does not provide a tool to inform management, but did provide a first step towards prioritising further work. The limited data available to inform parameters precludes the use of the sensitivity analysis results to inform the development of a European eel framework at this time, but the method is worthy of consideration for the sensitivity analysis anticipated for our framework.

Recently, a series of workshops have commenced to begin formal development of a conceptual model of population dynamics for *A. rostrata* (P. Angermeier, pers. comm.). This model describes limiting factors, relations between life-stages, and key uncertainties, as a prerequisite to identifying (via expert consensus) important variables and estimating parameters that can be used to run instructive numerical/simulation models.

2.6 Discussion

The models described above represent most of those that have been developed to simulate the dynamics of European and other eels. Due to the paucity of information on the life of eels in the sea, simulation work focuses on the freshwater phase. As shown above, the number of stages (glass eels, elvers, yellow, silver eels, and so on) that the models simulate and the detail in which the models describe each of the processes involved vary between approaches. This mainly reflects differences in the objectives of the modelling studies and in the approaches the studies adopt to handle the incomplete knowledge of the eel's life cycle. Although some of the models are more general than others with regard to the number of processes they describe and the way they describe them (such as SMEP and GlobAng), there is scope for further development and an increase in their level of sophistication. This is partly due to the complexity in eel dynamics and incomplete understanding of many processes, which means not only that a considerable number of processes need to be simulated, but also that more than one scenario needs to be modelled for each process.

Whilst both SMEP and GlobAng are highly relevant to our project, we considered SMEP to be a better starting point for model development since it already included descriptions of most of the processes of interest, and modifying those descriptions was expected to be easier than the addition of new processes (such as growth). In addition,

SMEP was developed by UK researchers who have considered the main characteristics of English and Welsh rivers and the processes that might affect eel dynamics in these rivers. Thus, the structure of the model is expected to be more appropriate to describe the dynamics of eel in the UK.

3 Development of the model framework

3.1 SMEP II - Model description

3.1.1 Overview

SMEP II is a software package developed to model the dynamics and exploitation of eel populations. It is based on the model (SMEP) originally developed by Bark, Knights, Kirkwood, El-Hosaini and Williams for Defra project CTG0102, further developed and tested during this Environment Agency-funded project. The model works on the scale of a river basin and consists of three main components:

- A model that simulates both the biological characteristics of the eel population and a number of potential anthropogenic influences on that population (the population dynamics model). Biological processes modelled include growth, natural mortality, sexual differentiation, maturation (silvering) and movements within the river basin. Anthropogenic influences include environmental and habitat quality, fishing practices, barriers to movement, and stocking.
- A GIS tool that helps the user determine the spatial structure that they want to use for their calculations and prepare the input files for the population dynamics model to run.
- A statistical model that is used to estimate some of the parameters of the population dynamics model.

The population dynamics model used in SMEP II is a length-based model that describes the dynamics of a population of eels for the duration of its stay in the river basin. The model is also sex-, life stage-, and area-specific and accounts for density-dependent effects and habitat structure and quality. The model does not include the dynamics of eels that have migrated from the river basin back to the spawning grounds (such as silver eels once they exit the river basin, or yellow eels moving back to saline waters (Tsukamoto and Arai, 2001)). Since only partial simulation of the population's dynamics is possible (the salt-water phase of population's life is not simulated, so no S-R relationship), processes such as recruitment cannot be modelled explicitly and, therefore, information about them needs to be provided externally (by the user).

The software is supplied with simple Excel (.csv) files that allow the user to easily identify the options available for each of the processes simulated and choose those they want to use. The software is also supplied with a series of pre-set input files and folders that need to be in place for the program to run (minimum set of inputs). If, for the options the user chooses, the model requires additional information to run, the user interface will provide directions on how to provide it. An Arc-GIS module is included as part of this package, which provides a simple way to define and describe the reaches in the river basin, assign numbers to them and calculate their length, wetted area and distance from the sea. In this way, the input files that define the reaches (including branching configuration) can be prepared automatically.

The Fortran 95 programming language has been used for the development of the population dynamics model, as this was the language used by Bark *et al.* (2007) in the

original development. SMEP was a single console (DOS) application and did not use any of the graphical features available with more recent versions of Fortran. Furthermore, the compiler originally used to create the executable program is now out of date. Therefore, the model was re-created (SMEP II) using the most up-to-date version of Fortran (Intel Visual Fortran). As part of this process, the source code is now separated into different sub-programs (modules). Code was added, and modifications to the existing source code were made to link the modules to each other. The source code has also been updated according to the standards of the new compiler. The model development also facilitates the creation of additional modules that can be 'bolted on' to the base model, to incorporate future developments such as a stocking module.

The model is available as an executable file, so users can run the model even if they do not have a Fortran compiler installed in their computer. However, for those that are interested, the source code is also available on request to Dr Alan Walker, Cefas.

The model can simulate the dynamics of the eel population under different assumptions about recruitment, environmental and habitat conditions, as well as initial conditions and the number of years over which the dynamics of the population will be simulated. The model projects the population forwards starting from a pre-defined initial condition (such as virgin conditions) (single projection) or can estimate the initial conditions and level of recruitment based on information about the status of the population at a specific year of the calculations (fitting the model to data, estimation of a single parameter). The statistical component of the software is used for the latter type of calculations. Options that allow the user to simulate fishing and impedance of movement or mortality associated with in-stream structures (barriers) are also available. The calculations are conducted assuming that all parameters are known without error (deterministic calculations). The only exception is when the model is fitted to data, in which case the model assumes that there is some uncertainty around these data. A more advanced statistical framework that will allow the estimation of more than one parameter simultaneously will be included in the next version of the software.

The following sections provide a detailed quantitative description of the formulae used to simulate the dynamics of an eel population and external factors that might affect it.

3.1.2 Population numbers

The number of individuals, *N*, in the system will change over time due to natural mortality, *M*; fishing mortality, *F*; recruitment of new eels in the river, *R*; and exit of silver eels from the system (moving to the sea). Each of these processes may affect eels of different length and/or life stage, and sex in different ways. The model uses three life stages to describe the population in the river: undifferentiated, and yellow and silver eels for which a further distinction is made between males and females. The model is length-based and as such, it assigns eels to different length classes and uses growth equations to determine how eels 'grow' from one length class to the next. Thus, at the beginning of each time step, τ, the number of eels in length class, *l*, and stage, *s*, will be calculated taking into account all the processes that are relevant to each stage of the eel life cycle (und=undifferentiated, y =yellow, sil = silver).

$$N_{l,s=und,\tau} = \sum_{l'=1}^{l} N_{l',s=und,\tau-1} \times G_{s,\tau-1}(l',l) \times e^{-(M_{l'}+F_{l'.s})} \times (1 - D_{l',g=f+m,\tau-1}) + R_{l,\tau} \quad (1a)$$

$$N_{l,s=y,g,\tau} = \sum_{l'=1}^{l} (N_{l',s=y,g,\tau-1} \times G_{s,\tau-1}(l',l) \times e^{-(M_{l'}+F_{l'.s})} \times (1-V_{l',g,\tau-1}) + N_{l',s=und,\tau-1} \times G_{s,\tau-1}(l',l) \times e^{-(M_{l'}+F_{l'.s})} \times D_{l',g,\tau-1}) \quad (1b)$$

$$N_{l,s=sil,g,\tau} = \sum_{l'=1}^{l} (N_{l',s=y,g,\tau-1} \times G_{s}(l',l) \times e^{-(M_{l'}+F_{l'.s})} \times V_{l',g,t-1} + N_{l',s=sil,g,t-1} \times G_{s}(l',l) \times e^{-(M_{l'}+F_{l'.s})}) \quad (1c)$$

where the definitions of the parameters shown above are as follows:

$G_s(l',l)$	Growth matrix that gives the proportion of eels in length class, l', and stage, *s*, to grow to length class, *l*, in one time step.
$D_{l,g,t}$	The proportion of eels in length class, *l*, that become yellow of each gender, *g* (differentiation), at any time step.
$V_{l,g,t}$	The proportion of yellow eels in length class, *l*, and gender, *g*, that becomes silver, in one time step.

The assumption used in the model for silver eels is that upon silvering they will try to leave the system at the next suitable time step. The model assumes that silver eel escapement takes place every year so that the silver eels calculated using formula (1c) will disappear from the system within a year from the time they become silver.

In one time step, eels can grow from one length class to the next, and they can also move from one reach to another. The sections below describe how the model simulates movement throughout the basin as well as the other processes included in our population dynamics model.

3.1.3 Definition of eels density in a reach

We have a limited understanding of how density affects the biology and dynamics of eels (though it appears to be an important force). The definition of the parameter that the user was required to provide in the original SMEP to determine when density-dependent processes take place was misleading. The parameter input file suggested that the B_{max} value represented the maximum sustainable biomass; that is, an upper limit to the biomass of eel that could be found in any reach. In reality, however, this value represents the local biomass at and above which density-dependent effects are maximal for all the relevant processes (growth, sex differentiation, movement, mortality). Thus, a clearer, more informative terminology has been adopted in SMEP II. Further, the formulae used to describe the effects of density on the relevant processes were reviewed and changes were made where necessary.

As mentioned above, the population dynamics model takes into account density effects when simulating the dynamics of eels. For the calculation, the density of eels in each reach is based upon their biomass rather than number. Expression of density as biomass per unit of space will not, however, provide enough information to allow comparison among the magnitude of density effects in each reach. This is because

each reach might be able to sustain different levels of eel density, and the effects of density for two reaches that have the same density of eels might therefore be different. To resolve this problem, an additional parameter, C_r, has been introduced which is used to define the values of biomass above which density-dependent effects achieve their maximum values for each reach. For each reach, the model calculates a relative biomass, $\hat{B}_r(\tau)$; that is, the biomass of the eels in a reach, B_r, divided by the reference biomass, C_r for the same reach. The model then uses the relative biomass as a proxy for eel density to calculate the effects of density on population dynamics. The user defines the reference biomass based on local knowledge or a default value (see section 3.3).

3.1.4 Movement

Area-specific saturation levels describe the effects of population density on processes such as sex differentiation, movement, mortality and growth. Because SMEP used a three month time step for the calculations, processes such as movement are applied once every three months. A finer temporal scale would allow a more realistic simulation of continuous processes. SMEP limited the silver eel emigration to four reaches per year. SMEP II allows the user to select a finer time step if it is necessary (for example to ensure that silver eels exit the river in the year when they mature). The source code has been modified so that the user has the option to specify the length of the time step externally.

SMEP used a spatially disaggregated approach for simulating movement of eel within the river, but assumed that the simulated reaches were part of the same linear river line such that they were placed one next to the other in a line. Thus, it could not simulate a branching river channel topology, a feature that will characterise most natural situations where eel populations are found in rivers. New source code has been developed to allow SMEP II to accept information about the branching connectivity of reaches in the form of a matrix (after Lambert and Rochard, 2007).

The formula used to calculate the proportion of yellow or undifferentiated eels that move from one reach to an adjacent one was modified to follow the model used by Lambert and Rochard (2007). The new formula describes movement that is driven by density and the ability of eels to cross obstacles and pass to adjacent reaches. So, contrary to the original formula in SMEP, the model does not use any other assumptions about directed movement to distribute eels among reaches.

Movement of undifferentiated and yellow eels

At each time step, the model calculates the number of eels that move from one reach to the next. The main assumption used for this simulation is that the movement of eels is affected by density levels in both reaches, the speed at which eels could travel, and their ability to pass any obstacles that they might encounter. In a single time step, an eel can only move from one reach to an adjacent one. The exception to this is for silver eels, which exit the system over one time step. The calculations used to simulate the movement of silver eels are described in a separate section below. So, for eels other than silver, the number of eels moving from one reach, r_1, to an adjacent reach, r_2, will be defined as follows:

$$\mathbf{N}(r_1 \rightarrow r_2) = N_{r_1} \times potential\ \ to\ cross\, reach\ \times prob\, to\ \ pass\, barriers(r_1, r_2) \times \\ density\ \ dependent\ \ tendency\ \ to\ move(r_1, r_2) \qquad (2)$$

Given that eels can move only from one reach to an adjacent one, care should be taken when reaches are defined to ensure that the length of the reach is comparable to (or greater) than the distance that eels would be expected to travel in one time step (see parameters review and user guide for more information).

Potential to cross a reach

The potential, $\theta(r,s)$, of eels in reach *r* and stage *s* to cross a reach is defined as the proportion of eels in the reach that are able to swim its length in one time step, τ. Stage, *s*, could be undifferentiated or yellow. Therefore, this proportion is easily calculated if we know the (average) speed, *u*(*s*), that eels at different stages could achieve and the length of each reach, Λ (*r*):

$$\theta(r,s) = \frac{u(s) \times \tau}{\Lambda(r)} \tag{3}$$

Programming-specific note: Given that we want to know if all eels can cross the reach in one time step (or if not, what proportion), and also that eels can move only one reach at a time, any values of $\theta(r,s)$ that are above 1 automatically mean that all eels could move outside the reach they occupy (that is, $\theta(r,s)$ is set equal to 1 when the result of the above calculation gives a value above 1 (see user guide)).

Probability to pass obstacles

Barriers and other obstacles could block or limit movement of eels from one reach to another. To account for this the model uses the probability to pass an obstacle, $b(r_1, r_2)$, when it calculates the number of eels that move from reach, r_1, to an adjacent one, r_2. The user needs to provide this probability as an input to the model.

Density-dependent tendency to move

The movement of eels from one reach to an adjacent one will depend on the relative biomass $\hat{B}_r(\tau)$ in each reach. The formula used to calculate the proportion of eels, $\phi(r_1, r_2)$, that will have the tendency to move from reach r_1, to reach r_2, as a result of differences in the relative biomass between the two reaches is described below (Whitehead, 2000; Lambert and Rochard, 2007):

$$\phi(r_1, r_2) = \frac{1}{\omega_{r_1}} \times \frac{d\ \hat{B}_{r_1}(\tau)}{C_{r_1} + d\ \hat{B}_{r_1}(\tau)} \times \frac{C_{r_2}}{C_{r_2} + d\ \hat{B}_{r_2}(\tau)} \tag{4}$$

Where:

ω_r is the number of reaches that are adjacent to reach, *r.* An example of the possible branching configurations is shown in Figure 3.1. In this example, reach 1 has only one adjacent reach while reach 2 has five adjacent reaches. Guidance on the rules that need to be followed when assigning numbers to the reaches is provided in the user manual (see Chapter 5).

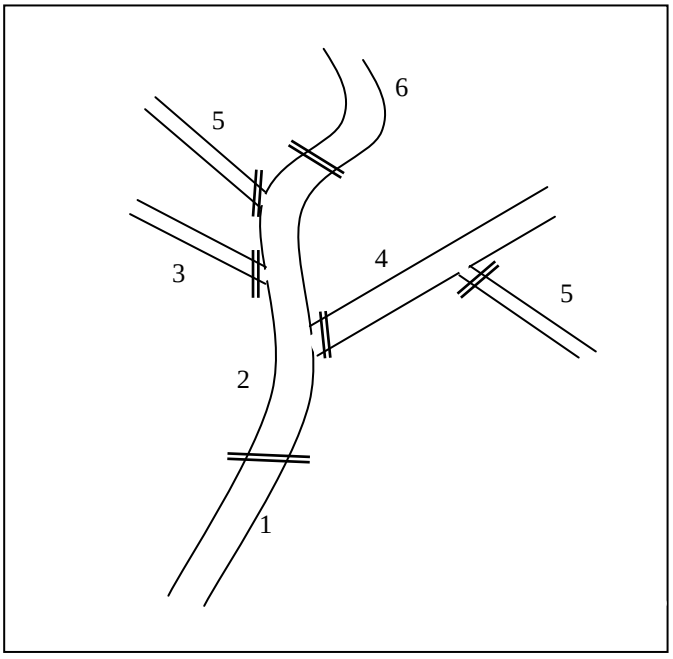

Figure 3.1. A possible branching configuration and selection of reaches when considering eel movements in a river

d is a constant that describes the relative influence of the density levels in the reaches that the eel is moving 'from' and 'to', or the donor and recipient reaches. For very small values of *d,* the density level in the recipient reach does not affect the proportion of fish that move into it. The bigger the value of *d,* the more sensitive the simulation becomes to the relative difference between densities in both reaches, and the proportion of fish moving to a reach is affected less by the density levels in the donor reach. In addition, for values of *d* that are big enough to be comparable to (or greater than) the reference biomass, $C_{r,}$ the proportion of fish moving to a reach becomes almost insensitive to changes in density levels ($\hat{B}_r$) once the density biomass in the donor reach exceeds that of the reference biomass.

Silver eel migrations

The main assumption used for the simulation of the movement of silver eels is that they have a tendency to exit the system as soon as possible. Therefore, the number of silver eels that leave the system is determined by the ability of a silver eel to cover the distance between the reach where it resides when it becomes silver and the sea within a year (or less if the window of time when silver migration is allowed is smaller than a year). The simulation of this movement also takes into account any barriers that silver eels might encounter. We only simulate a downstream movement and the number of silver eels that move from reach, *r*, to another one closer to the sea will be:

$$N_{s=silver,\tau}(r \rightarrow r') = N_{s=silver,\tau-1}(r) \times \theta(r, s = silver) \times b(r, r') \qquad (5)$$

3.1.5 Gender differentiation

The model assumes that all eels differentiate at the same length, L_D, but the proportion of the differentiating eels that become male or female depends on the relative biomass (density) of eels in their reach. Two different types of ogive curves can be chosen to describe that dependence. Figure 3.2 shows the two types of curves (type I and type II), and their mathematical descriptions are provided below. Each ogive curve is formed by two parts; for both ogive curve types, the coordinates of the inflection point (the point where the two parts of the curve connect) are always (0.5, 0.5). A shape parameter, called ρ for Type I curves and λ for Type II curves defines the shape of the curves. The maximum value that each of the two family of curves could take is equal to $0.5+\delta$ while the minimum value is equal to $0.5-\delta$, where δ is a constant and can take values between 0 and 0.5. Thus, the user could change the upper and lower value that the curves reach by modifying the value of the constant, δ.

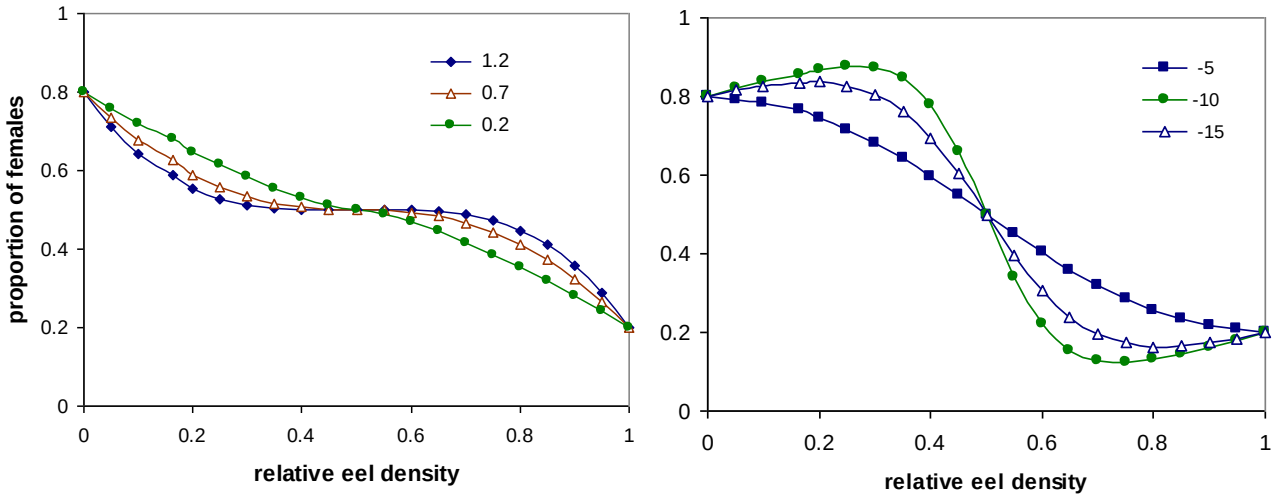

Figure 3.2. Types of curves that the model can use to describe the proportion of differentiating eels that become females at different levels of relative density.

Left panel: Ogive type I, Right panel: Ogive type II. The numbers in the captions correspond to different values for the model parameter (ρ for Type I curves and λ for Type II curves) that determines the slope of the curves.

Type I

$$D_{l,g=f,\tau} = \begin{cases} 0.5 + \dfrac{\delta}{0.5^{2\times\rho+1}} \times (0.5 - \hat{B}_{s=und,\tau})^{2\times\rho+1}, & if\ \hat{B}_{s=und,\tau} \le 1 \\ D_{l,g=f,\tau}(\hat{B}=1) = 0.5-\delta & if\ \ \hat{B}_{s=und,\tau} > 1 \end{cases} \quad (6)$$

Type II

$$D_{l,g=f,\tau} = \begin{cases} \frac{1}{1+e^{-\lambda\times(\hat{B}_{s=und,\tau}-0.5)}} + (|0.5+\delta| - \frac{1}{1+e^{0.5\times\lambda}}) \times \frac{0.5-\hat{B}_{s=und,\tau}}{0.5}, & if\ \hat{B}_{s=und,\tau} \le 0.5 \\ \frac{1}{1+e^{-\lambda\times(\hat{B}_{s=und,\tau}-0.5)}} - (\frac{1}{1+e^{-0.5\times\lambda)}} - |0.5-\delta|) \times \frac{\hat{B}_{s=und,\tau}-0.5}{0.5}, & if\ 1 \ge \hat{B}_{s=und,\tau} > 0.5 \\ D_{l,g=f,\tau}(\hat{B}=1) = |0.5-\delta| & if\ \hat{B}_{s=und,\tau} > 1 \end{cases} \quad (7)$$

Thus, for values of the relative density that are close to 0.5, ogive II results in far greater changes in the proportion of females for relatively smaller changes in density (relative biomass). On the contrary, ogive I describes sharp changes in $D_{l,g,t}$ for relatively smaller changes in density for values of the relative biomass that are close to 0 or 1.

The formula that SMEP used to calculate the proportion of undifferentiated eels that become females assumed that this is always close to 1 at very low densities, and declines to 0 for densities that are higher than a reference value. However, a review of information on the proportion of undifferentiated eels that become males or females indicates that some females might be produced even at very high density levels (see section 3.3). Equally, it is not clear if males are produced at very low densities. The original formula was modified, therefore, to allow for more flexibility in the way in which the differentiation process is described. SMEP II includes a new parameter that allows the user to specify the maximum and minimum proportion of females produced at extreme density conditions. Essentially, the types of curves are the same but the upper and lower limits can be modified depending on the situation that we want to simulate. This is of importance for testing different sensitivity analyses and to be able to capture some of the hypotheses about the effects of density that experiments and field studies reported in the literature.

3.1.6 Growth

The von Bertalanffy (VBF: Beverton and Holt, 1957) growth equation is often used to describe the growth of several fish species, and was used in SMEP. However, as there are indications that growth of eels might not be described well by a von Bertalanffy function (see section 3.3), and to provide more flexibility in the simulation of eel growth, the model provides three different sets of equations that can be used to simulate the growth of eels. These are a linear function, the VBF and the Schnute family of growth curves (Quinn and Deriso, 1999). All these functions can describe the length of an animal at a given age. Given that our model is length-based, the information that is required by the model is the increase in the length of an eel of length, *L*, within a specified time period. So, all formulae were re-parameterised to give the increase in length in a time period rather than actual length-at-age. The formulae are shown below:

Linear model:

A linear model assumes that there is a constant increase, *g*, in the length of eels over time. Therefore, the increase in length, ΔL, over a time period, τ, will be:

$$\Delta L(L,\tau) = g \times \tau \tag{8}$$

VBF model:

$$\Delta L(L,\tau) = (L_{\max} - L) \times (1 - e^{K \cdot \tau}), \tag{9}$$

Where L_{max} is the maximum length that eels can attain and K is a parameter that determines the rate of increase towards $L_{max.}$

Schnute model:

The Schnute model consists of four different formulae, each of which describes different growth behaviours. Although the linear and VBF models are sub-cases of the Schnute model, they have also been set up separately to make their use easier. The four equations are:

$$\Delta L(L,\tau) = \left[\ L_1^{\gamma} + L^{\gamma} \times \chi_1 + \frac{(L_2^{\gamma} - L_1^{\gamma} + (L_1^{\gamma} \times \chi_2 - L_2^{\gamma}) \times \chi_1)}{1 - \chi_2}\ \right]^{1/\gamma} - L \tag{10a}$$

where $\chi_1 = e^{-k \cdot \tau}$, $\chi_2 = e^{-k \cdot (\tau_2 - \tau_1)}$ and γ and k are constants that determine the type of curve that is used to describe growth. If both γ and k are not 0 then the above formula is used. Otherwise, one of the following three formulas applies. L_1 and L_2 are the lengths of eels at time τ_1 and τ_2, respectively.

$$\Delta L(L,\tau) = L_1 \times e^{\frac{1-\chi_1}{1-\chi_2} \cdot \ln\frac{L_2}{L_1} + \chi_1 \cdot \ln\frac{L}{L_1}} - L, \qquad \gamma = 0 \tag{10b}$$

$$\Delta L(L,\tau) = \left[\ L^{\gamma} + \frac{(L_2^{\gamma} - L_1^{\gamma}) \cdot \tau}{\tau_2 - \tau_1}\ \right]^{1/\gamma} - L, \qquad k = 0 \tag{10c}$$

$$\Delta L(L,\tau) = L \times (e^{\ln(\frac{L_2}{L_1}) \cdot \frac{\tau}{\tau_2 - \tau_1}} - 1), \qquad \gamma = 0 \text{ and } k = 0 \tag{10d}$$

Examples of each of these growth curves are presented later in this report (Figure 4.6).

The SMEP II model allows the user to specify stage-specific parameters for the growth equation. If this option is chosen, the user will need to provide one set of parameter values for undifferentiated eels and another for differentiated eels, which may be specified for male and female yellow eels.

Each of the formulae described above calculate the increase in length for an eel of length, L, in time step, τ. Each length class includes eels of different lengths so the increase in their length in one time step will vary. In order to find the proportion of eels from one length class that grow to another, each length class is broken down into smaller sections (sub-classes), small enough that the increase in the length per time step of all eels in a sub-class is almost the same. Using the increase in length that corresponds to each sub-class, we can easily calculate the length-class to which eels will move in a time step.

3.1.7 Natural mortality

A Weibull distribution is used to describe natural mortality, *M*, at length (De Leo and Gatto, 1995). In its simplest form, this formula has two parameters: the maximum length, L_{max}, and the Weibull parameter, ν :

$$M(L) = \nu \cdot \left(\frac{L}{L_{\max}}\right)^{\nu-1} e^{-\left(\frac{L}{L_{\max}}\right)^{\nu}}, \quad L \geq 0 \tag{11a}$$

The formula above uses the length of eels to calculate the natural mortality that corresponds to their length. A second formulation of the Weibull function can also allow for density effects, as follows:

$$M(L,\hat{B}) = \nu'\left(\frac{L}{L_{\max}}\right)^{\nu'-1} e^{-\left(\frac{L}{L_{\max}}\right)^{\nu'}}, \qquad L \geq 0 \tag{11b}$$

where

$$\nu' = \begin{cases} \hat{B}\cdot(\nu_{\max} - \nu_{\min}) + \nu_{\min}, & \hat{B} \leq 1 \\ \nu_{\max}, & \hat{B} > 1 \end{cases} \tag{11c}$$

The model uses both parameterisations of the Weibull function: the density-independent formula is used to calculate the mortality of differentiated eels, while the density-dependent option is applied to calculate the mortality at length for undifferentiated eels. The changes in the shape of the mortality curve for different values of ν and levels of eel density are shown in Figure 3.3.

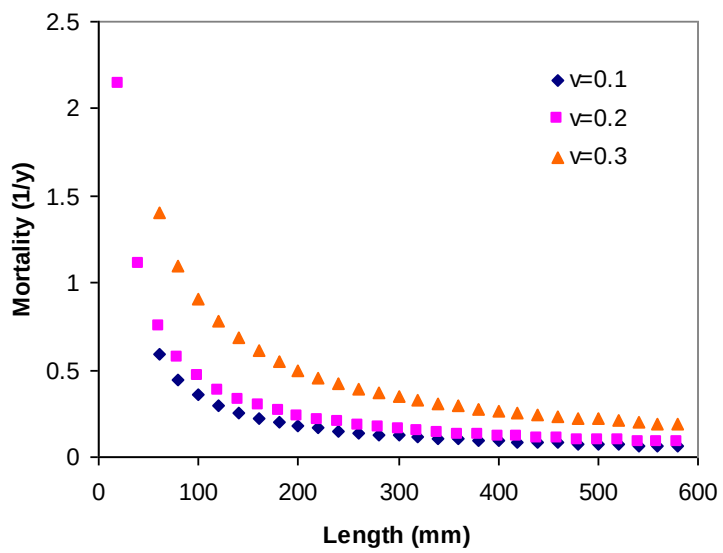

Figure 3.3. Weibull curves for three different values of the parameter ν. If density effects are taken into account, and ν_{min}=0.1 while ν_{max}=0.3, the curve that corresponds to ν=0.2 would give the values of M when the biomass of the relevant group (i.e. undifferentiated) was equal to 50 per cent of its reference biomass.

The formulae used to describe *M* give the mortality for eels of different length. As with the calculation of growth, these values are used to determine the value of *M* that corresponds to each length class. The Simpson method (Simpson and McGilchrist, 1980) is used to sum over the mortality values that correspond to the range of lengths included in each length class. A brief description of the steps followed for that calculation is given in Appendix II.

A graphical representation of the range of natural mortality values for each length class that seem reasonable according the literature is provided in Figure 3.4.

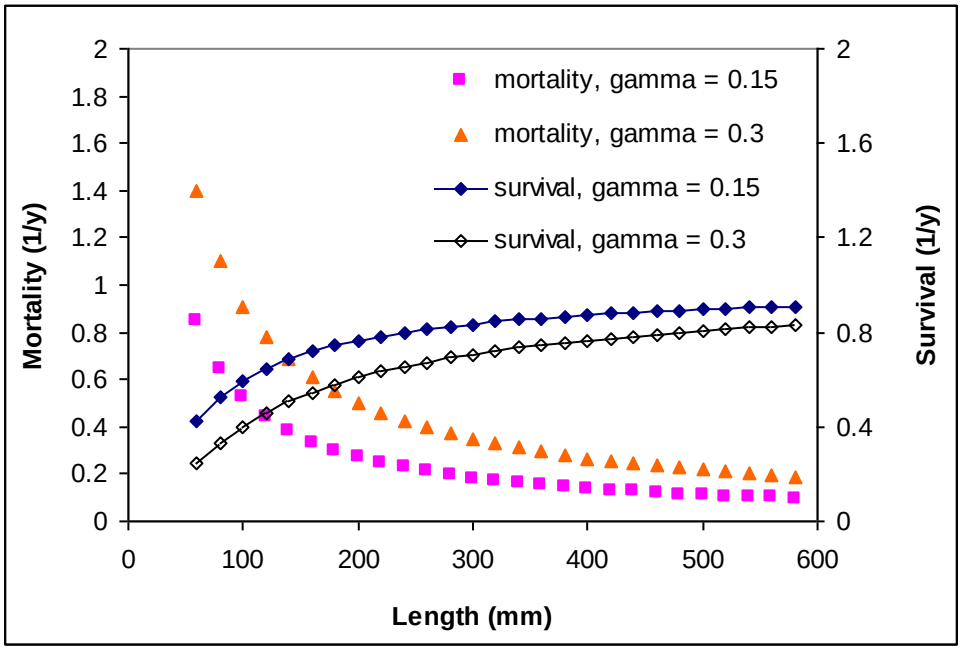

Figure 3.4. Functions of natural mortality-at-length, and corresponding survival rates, for extreme mortality 'gamma' values. The two lines of coloured symbols for natural mortality define the range of values of natural mortality that are allowed for each length. Similarly, the two solid lines define the maximum and minimum values of mortality and survival for each eel length that SMEP II applies, depending on the levels of density of eels relative to the Critical Density (that is, MaxBDensity in the Parameters.csv file: see Chapter 5).

3.1.8 Silvering

The model uses a logistic equation to describe the proportion of yellow eels that silver at each length:

$$V_{l,g,t} = \frac{1}{1+e^{-\alpha_g \cdot (l-\eta_g)}}, \qquad (12)$$

where a_g and η_g are constants and are gender-specific. In this way, the model allows for gender-specific maturation (Figure 3.5). As with natural mortality, the Simpson formula is used to calculate the proportion of yellow females and males in each length class that will become silver.

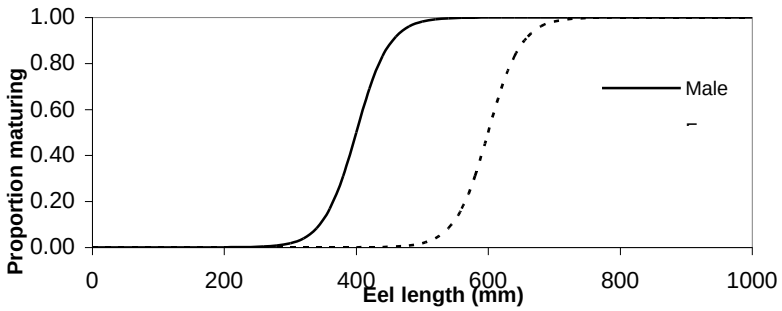

Figure 3.5. Single logistic functions for maturation at length for both males and females.

3.1.9 Fishing

Fishing can be described in SMEP II in two ways, depending on the available data: numbers caught by length class per gear type; or numbers caught by stage (undifferentiated, yellow or silver) per gear type. All fishing data are related to reaches, seasons and years. Therefore, it is possible for the user to vary both the location and impact of fisheries, and simulate changes in the control of fisheries.

3.1.10 Recruitment

Recruitment refers to the number of eels (usually glass eels) arriving at the mouth of a river basin each year. Due to the lack of knowledge regarding the oceanic phase of the eel's life cycle and no observed spawner-recruit relationship, the model will only add recruitment in formula (1a) if relevant information has been provided by the user. The information that the model needs in this case is the number of recruits, their length distribution (defined by the mean and standard deviation), and the upper and lower lengths of this distribution. The model then allocates the number of individuals across this length range, based on the assumption that recruit lengths are normally distributed between, and within, each length class.

3.1.11 Reference biomass and habitat quality

As mentioned in section 3.1.3, each reach in a river basin is characterised by a reference biomass of eels that is used to calculate the relative biomass in each reach in order to determine the effects of density on population dynamics. To calculate the reference biomass per reach, the model multiplies the reference biomass density by the wetted area of that particular reach. Both the reference biomass density and wetted area are provided by the user as inputs to the model. The reference biomass, C_r, can then be multiplied by an environmental and habitat quality index to take account of annual environmental and habitat effects on the capacity (in terms of the biomass of eels it can sustain) of each reach. If the environmental and habitat quality index varies

annually, the effects of density on the eel population in a given reach will also be expected to change from year to year, even if the density of eels in the reach does not.

3.2 User inputs to model framework

3.2.1 User interface

The user interface, associated input files, and output files for the model results are fully described in Chapter 5, but briefly described here.

River reaches are defined by the user according to their length, wetted area, distance from the sea and their connectivity to neighbouring reaches. In SMEP, such information for each reach was derived manually, either from measurements of maps, digital images or from fishing survey width data. We have developed a GIS-user interface for SMEP II which automates most of this process and thereby assists the user in creating the input matrix. The GIS module provides a simple mapping tool which allows users to split a river into a number of reaches labelled according to their distance from the sea, calculate reach length and wetted area, and construct a connectivity matrix including a qualitative level of structural impedance to migrations.

In addition to the GIS tool that has been added to the model framework, the input files that are part of the interface have been extended to allow the user to specify the types of formulae and parameterisation of a greater number of processes simulated in the model. Additions in the input files are:

- The user can specify the type of growth model that will be used for the formulation and provide the values of its parameters.
- The user can specify the maximum and minimum value of the curve that describes the proportion of differentiated eels that become females.
- The user can specify whether the normal distribution that describes the recruitment at length should be truncated, and the appropriate maximum and minimum values of length.

More importantly, the user is not required to set the structure of the model and provide information once the model has started running. The original model used a set of input windows which would instruct the user to provide specific information about the structure of the model, spatial configuration, anthropogenic factors to be considered, and so on. All this information can now be inputted into an excel file prior to running the model so the user does not need to provide any data in real time. This has increased the speed of the calculations and also makes it easier to repeat the calculations and therefore reduces the risk of user-entry errors.

3.2.2 Supporting material

The focus of our work has been on developing more hands-on tools that will support the user guide and the model description documents. For this purpose, we have created Excel spreadsheets which describe how key formulae used in the model behave (that is, illustrate results) and which can help the user choose the parameterisation of the model which best describes the behaviour they want to simulate. This material will be supporting material that will be provided together with the model. We have also documented all the new processes added into the source code and added references to relevant published material that provides more information on the formulae that were used in the original SMEP.

4 Description of processes and selection of parameters

4.1 Introduction

The objective of this project is to develop a parameterised life-history model that can be applied to eel stocks in English and Welsh rivers in order to quantify reference levels and compliance with the management target required by the European Council eel regulation (Eel Recovery Plan). The model applies the life processes of growth, sex differentiation, natural mortality and maturation to individual eels, along with the movement of individuals throughout a river basin, in order to simulate the production of eels from within that basin.

Ideally, when applying the model to a data-rich basin, the user will set the parameter values for these processes according to those measured for the study population. In most cases, however, such knowledge will not be available for the study population, and the user will have to apply default parameter values. The user requires, therefore, an understanding of potential default parameter values that are available in the scientific literature.

In this chapter, we consider what is known about these processes, based on a review of the literature and on our own analyses of UK eel data made available by the Environment Agency and Defra (such as Bark *et al.*, 2007). We use this knowledge first to describe the form of the processes and hence the manner in which they are dealt with by the model, and second to provide a range of default parameter values that users can apply in data-poor situations. Different default values may be required for pristine and present-day scenarios, where density effects do or do not occur, and for different habitats (relating to productive potential), both within and between river basins. Recruitment (or settlement) trends and quantities are also required.

We have focused primarily on information from studies of European eel (*Anguilla anguilla*), but also consider information from other Anguillid species where that information may provide useful detail on the processes and their drivers that may be common between species. Where we refer to ‘eel’ in the report, that always means European eel; for other species, we provide the species name. Whilst we have attempted to deal with a particular process in each sub-section, they are inextricably linked and some overlap is unavoidable.

4.2 Growth

Growth in eels has been the focus of many studies, either directly or as a subsidiary to other objectives. Efforts to describe general growth patterns for populations are hindered by high levels of variation between individual eels and, sometimes, within growth trends of individuals.

4.2.1 Describing growth – the form of growth model

Growth of eels is modelled by SMEP II as a change in length over time. SMEP described this function using the von Bertalanffy (vB) growth model (von Bertalanffy, 1938, after Beverton and Holt, 1957). For SMEP, the user was required to define the L_{max} and *K* parameters (but not the L_0 parameter; that is,length at birth): see section 3.16 for explanation of the parameter symbols.

A number of studies have used the vB formula to describe eel growth (Bisgaard and Pederson, 1991; Mann and Blackburn, 1991; De Leo and Gatto, 1995; De Leo and Gatto, 1996; Poole and Reynolds, 1996b; Tzeng *et al.*, 2000; Lin *et al.*, 2007; Simon, 2007), though few authors report testing the goodness of fit of the vB function to their data (De Leo and Gatto, 1996; Poole and Reynolds, 1996b).

Growth patterns vary considerably between individuals within populations, with the result that many studies fail to derive robust growth curves (Moriarty, 2003). A linear growth form may be an appropriate approximation throughout much of the length range of eel species (Barak and Mason, 1992; Jellyman, 1997; Svedang, 1999; Aprahamian, 2000). For example, a linear relationship explained between 65 and 89 per cent of the variation in growth of eels in lower Severn sites (Aprahamian, 2000). Eels from six lakes in the Havel system in Germany were shown to grow relatively quickly in their first two years, but then adopted almost constant annual increments across the subsequent 12 years (Simon, 2007). Though exponents of the vB growth model, Poole and Reynolds (1996b; 1998) observed that the largest silver eels in their samples showed slightly higher than normal growth rates at a young age and maintained these levels up to capture at migration (that is, linear growth), whereas most of the other eels showed growth rates that 'flattened out' as they aged, and took longer to reach maturity (for their size).

It is suggested that the relationship between growth rate, the available food resources and the partitioning of energy determines the point of optimum size and energy reserves for reproduction (Poole and Reynolds, 1998; Broad *et al.*, 2001). Hence, where resources are not limiting, growth may be better described by a linear form (Moriarty, 2003).

Analyses of growth data may be compromised by the biases inherent in sampling the non-migrating component of populations (Rasmussen and Therkildsen1979, cited by Bisgaard and Pederson, 1991). As silvering in eels depends on size, rather than age, fast-growing eels start their spawning migration earlier than slower growing individuals, and the latter may therefore be over-represented in higher age categories (Lamson *et al.*, 2009). Thus, the vB function may be an unnecessarily complicated model with which to describe growth in eels.

To investigate this further, we used length at age data (Defra-Kings, after Bark *et al.*, 2007) from rivers Blyth, Ellen, Colne, Blackwater and Hull to explore the fit of a number of length-at-age formulae including vB and linear functions. As explained above, slower growing individuals may be over-represented in the higher age categories of non-silvering eels, and our analysis was restricted to younger individuals, using a cut-off age of 15 (following Oliveira and McCleave, 2002; Jessop *et al.*, 2004; Lamson *et al.*, 2009).

In all cases, the linear equation has either the best fit in the data or was very similar to the one that achieved the best fit (Figure 4.6). Given that the linear growth function is the simplest and there are concerns about the paucity of information on the growth of eels above a certain length, we have chosen to use a linear relationship to describe the growth of eels in SMEP II.

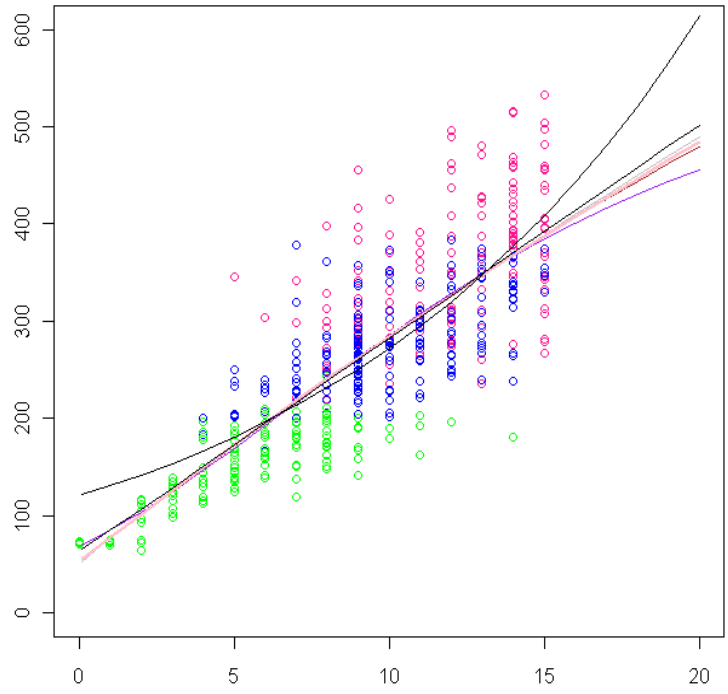

Figure 4.6. Fit of different growth models to length (y axis: mm) at age (x axis: year) data from four rivers. The green, blue and red symbols represent data for undifferentiated, male and female eels, respectively. The red line corresponds to the linear model, the purple line corresponds to the VBF model, and the other lines correspond to several forms of Schnute models

4.2.2 Comparison of stages and genders

Stage-specific

In their process-driven model of eel production in the Comacchio lagoons, Italy, De Leo and Gatto (1995; 1996), assumed that gender was already 'decided' at recruitment and hence that gender-specific variability in growth of individuals was operating at the age of recruitment (that is, age 0, mean length 75 mm). This had the effect of over-emphasising differences in rates of growth (length-at-age) and silvering between the two sexes. Melia *et al.* (2006a), therefore, applied a third growth function, for undifferentiated eels, in their modelling of the age and growth of eels in the Camargue lagoons, France. Although they chose to represent undifferentiated growth using the vB model/function, Melia *et al.* (2006a) accepted that this was mainly to be consistent with the form of their description of growth for males and females, and that a linear growth shape was equally appropriate to their data.

Gender-specific

Though there are reports of males growing faster than females (Holmgren *et al.*, 1997), female eels tend to have higher growth rates and to continue to grow for a longer time than males, both in European eels (Sinha and Jones, 1967; Aprahamian, 1988; Mann and Blackburn, 1991; Poole and Reynolds, 1996b; Holmgren *et al.*, 1997) and in other Anguillid species (Jellyman, 1997; Jessop *et al.*, 2004; Walsh *et al.*, 2006).

Holmgren and Mosegaard (1996) observed that males were shorter than females of the same age, even in low weight groups, and suggested that males put on weight (muscle and fat build up) at the expense of growth in length, whereas females increase in length and then weight (skeleton growth before muscle or fat). Developing this further, Broad *et al.* (2001) suggested that females adopt a size maximising strategy to ensure high fecundity on reaching the spawning area, whereas males adopt a strategy to reach migration size as quickly as possible.

This apparent difference in growth rates between males and females would suggest the need for sex-specific growth formulae in our model. However, the reported differences are often minor (Sinha and Jones, 1967), and we therefore compared the growth rates of male and female eels sampled in rivers of England and Wales (Bark *et al.*, 2007) to test whether they supported the use of sex-specific or a generalised growth function.

4.2.3 Habitat effects on growth rates

Across the UK, mean annual length increments of eel populations (sexes pooled) from fluvial sites within river basins have ranged from 13 to 58.7mm (Aprahamian, 1988; Mann and Blackburn, 1991; Naismith and Knights, 1993; Aprahamian, 2000; Knights *et al.*, 2001; Bark *et al.*, 2007; Chadwick *et al.*, 2007). In Ireland, published mean annual increments range from 13.8 to 42mm (Poole and Reynolds, 1996a, b; 1998; Arai *et al.*, 2006). In Scandinavia, annual increments of 24.5 and 62mm have been reported (Vollestad and Jonsson, 1988; Bisgaard and Pederson, 1991).

Fewer studies report growth rate of eels in still waters from northern Europe, but mean annual increments of 22 to 36.7mm were reported for eels from lakes in the Erne catchment (Ireland) (Arai *et al.*, 2006), 45 to 53mm for eels in German lakes (Simon, 2007), and as high as 60 to 73mm for lakes in south-eastern England (Naismith and Knights, 1993), and Sweden (Holmgren *et al.*, 1997).

Studies from northern European saline waters have reported mean annual length increments ranging from 25 to 79mm (Naismith and Knights, 1990; 1993; Pedersen, 1998; Arai *et al.*, 2006; Daverat and Tomas, 2006; Bark *et al.*, 2007; Lin *et al.*, 2007).

Growth of eels largely depends on temperature and food availability (Jellyman, 1997). The optimum temperature for growth in eel is 20-26ºC (Tesch, 2003), and growth typically ceases at temperatures below 10ºC (Elie and Daguzan, 1976). The thermal regime affects growth potential depending on the length of the growing season, although growth rates are not correlated with latitude (Jellyman, 1997). Water temperatures in rivers of England and Wales rarely exceed 20ºC for more than a few days during the summer (Cefas, unpublished data), however, so there is little to be gained from comparing growth over months between rivers depending on the time when temperatures are in the range 20-26 ºC. Rather, the number of days when temperatures exceed 14ºC-16ºC is often considered to be more relevant (Deelder, 1984; Tesch, 2003).

Saline vs freshwater

Generally, growth rates of eels are faster in saline than in freshwater environments, both in European eel (Acou *et al.*, 2003; Daverat and Tomas, 2006; Melia *et al.*, 2006b; Bark *et al.*, 2007; Lin *et al.*, 2007) and in other anguillid species (Tzeng *et al.*, 2003; Arai *et al.*, 2004; Jessop *et al.*, 2004; Walsh *et al.*, 2006; Lamson *et al.*, 2009). In the UK, for example, eels from the River Piddle and Tadnoll Brook (tributary of the Frome) grew on average at about 20mm per year, whereas those from their joint estuary, Poole Harbour, grew at about 40mm per year (Bark *et al.*, 2007). Mean back-calculated annual lengths-at-age for American eels, *A. rostrata*, were 94mm in seawater, 60.5mm in tidal waters and 44.2mm in freshwater residents (Lamson *et al.*, 2009).

These differences may be due to the overall higher productivity of the saline compared to the freshwater environment, and also to the more favourable thermal regime resulting in a longer growing season (Naismith and Knights, 1993; White and Knights, 1997; Melia *et al.*, 2006a; Shiao *et al.*, 2006; Walsh *et al.*, 2006; Lamson *et al.*, 2009).

The differences are not always so great. Eels in the River Wnion (Wales) grew at an average annual rate of 18.4mm but those sampled in the Mawddach estuary downstream had a rate of 24.5mm (Bark *et al.*, 2007).

Movement of eels between salinity zones means that the habitat where yellow eels are captured does not necessarily represent the habitat utilised during their entire growth phase (Lamson *et al.*, 2009). Thus, the differences reported above may be associated with an incorrect assumption about the origin of the eels sampled, in both rivers and estuaries, and comparisons of habitat effects on growth rates should only be compared between eels of known origin. For those sampled in estuaries, the amount of time spent in saline versus freshwater habitats can be inferred from microchemical analysis of strontium and calcium levels in the otoliths (Daverat *et al.*, 2004; Arai *et al.*, 2006; Shiao *et al.*, 2006). Nevertheless, the growth characteristics of an eel population – whether in freshwater, an estuary or in the sea – are those required by the model. Introducing growth histories in proportion to movements between different habitats would add a complexity that may be self-defeating in terms of precision or accuracy.

Comparisons within and/or between river basins of England and Wales

Though a considerable range of growth rates has been reported between rivers across Europe, mean annual length increments of eels sampled in 14 English and Welsh rivers are similar, ranging from 16 to 28mm (Aprahamian, 1988; Aprahamian, 2000; Knights *et al.*, 2001; Bark *et al.*, 2007), though rates from some lower tributaries of the River Thames reached 58.7mm (Naismith and Knights, 1993). This suggests that it would be reasonable to apply a single description of growth when modelling eel populations for the majority of rivers in England and Wales. This is certainly a practical advantage, since new growth data for previously unsampled rivers can only really be collected by destructive sampling of larger numbers of eel, which is to be avoided where possible during this time of low recruitment.

It is reasonable to assume that conditions influencing growth are different between sites near to the sea and close to the source of a river. However, we could find no reports in the literature of comparison of growth rates between sites throughout a river system. Though Bark *et al.* (2007) surveyed eel in about 10-20 sites each in 14 rivers, only a few eels (<24, means of 5 to 13 across rivers) were aged from each site in order to calculate whole-river mean growth rates, and their data are insufficient to examine potential variation in growth rates between sites within a catchment or between the sexes.

4.2.4 Density-dependent effects on growth

Given that growth is likely to be resource-limited, it is reasonable to assume that there may be an effect of density on growth rates. However, it is difficult to quantify a density-dependent effect in the natural environment because of fluctuations in local populations and environmental conditions. Few studies have even considered evidence for such an effect, let alone attempted to quantify the relationship between density and growth.

Using their model (De Leo and Gatto, 1995) to estimate density of eel within the Valli di Commacchio lagoons in northern Italy, De Leo and Gatto (1996) inferred a density-dependent effect on growth rates because the average size of yellow eels was smaller during a period of years when lagoon densities were relatively high (3388 eels.ha^{-1}, 149 kg/ha^{-1}) when compared to a period of relatively low density (597 eels.ha^{-1}, 55 kg.ha^{-1}). Note, however, that this difference could also be explained as an artefact of the increased proportion of small eels resulting from higher recruitment levels.

Aprahamian (2000) found no relationship between variation in mean growth rates (16.36 to 27.92mm.yr^{-1}) of eel in 15 sites throughout the lower tributaries of the River Severn, and order of magnitude variations in either density (10 to 120 eels.100m^{-2}) or biomass (250 to 2550g.100m^{-2}) measured at these sites. He suggested that these sites had all reached carrying capacity, for eel growth at least.

The rates measured by Aprahamian are well below the maximum reported for European eel in rivers but similar to those of other studies of UK and Irish waters (see Aprahamian, 2000; Bark *et al.*, 2007; 2009). Unfortunately, this is the only study of eel in UK rivers where sufficient site-specific data were collected to allow a robust comparison between sites within a single basin, and all the sites were close to the estuary.

Interestingly, the range of mean growth rates measured by Bark *et al.* (2007) for eel in 14 English and Welsh rivers is very similar to that measured by Aprahamian (2000) for lower Severn tributaries. As the Bark *et al.* data pooled eels sampled from survey sites throughout lengths of the rivers (as opposed to Aprahamian (2000) where growth rates was estimated at the site level), it is unlikely that all the sites sampled by Bark et al were at their productive potential and therefore that these growth rates are all limited by density *per se*, but they were presumably limited by environmental factors. As such, we have not treated the Aprahamian (2000) rates as representative of density-limited growth rates in SMEP II.

4.2.5 Length-weight function

SMEP II is primarily a length-based model, as most of the processes appear to be affected by the length of the fish, and because length is easier to record than age (which requires destructive sampling) and is therefore more likely to be available for the study population. As the target for EMPs has been set as silver eel biomass, however, it is necessary to convert the length-based model outputs to a weight. This is achieved by applying a length-weight relationship. Separate relationships have been developed for undifferentiated + yellow and for silver eels, because silver eels appear to be relatively heavy for a given length, presumably due to the high levels of lipid stored for the oceanic migration.

The relationships were derived from measures of 24,063 undifferentiated and yellow eels collected from freshwater reaches of 13 rivers by Aprahamian (1988) and Bark *et al*. (2007) over the period 1983 to 2004, and 723 silver eels from five rivers sampled by Aprahamian, Bark *et al.* and by Cefas during this and other recent Defra and EU-

funded projects. Both multiple regression and non-linear regression models were tested. Although separate curve forms are derived from the yellow and silver eel data, visual examination of the data spread and the two curves (Figure 4.7) suggests that there is very little difference in the relationships for eels less than 650mm in length. Therefore, a single, yellow eel, length/weight curve form is applied in SMEP II.

For the yellow eel data, which included pre-silvering eels, we found the better fit to the data using a nonlinear least squares method to estimate parameter values for the relationship:

$$\text{Weight} = A.\text{Length}^{B}$$

where $A = 5.421e^{-7}$ and $B = 3.196$

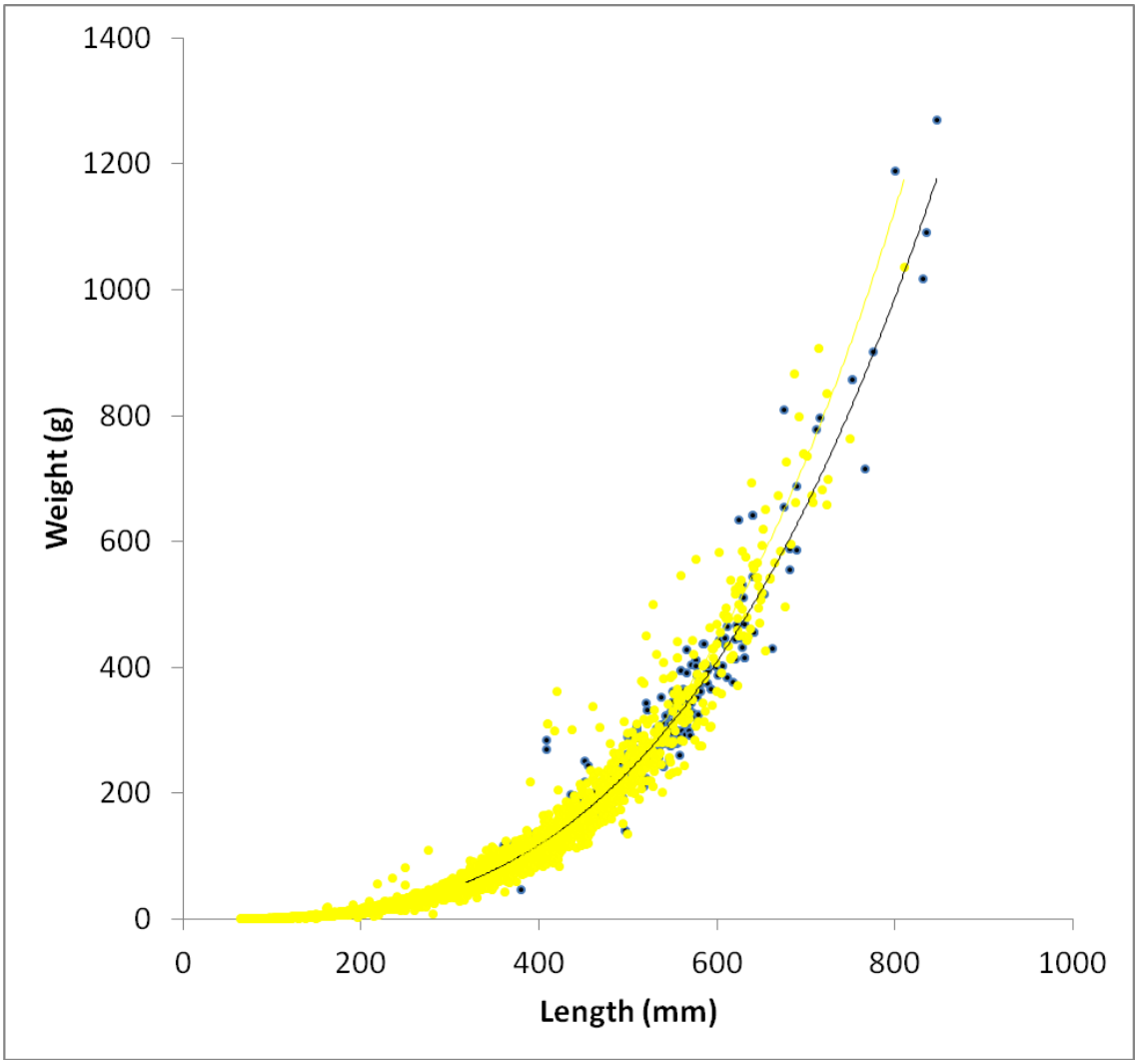

Figure 4.7. Length-weight distributions for yellow and silver eel from English and Welsh rivers. Yellow eels are shown by the yellow circles and yellow trend line; silver eels are shown by the black circles and black trend line.

4.3 Gender differentiation

The biological mechanism by which individual eels become male or female is not well understood, but was recently reviewed by Davey and Jellyman (2005). The sex of developing gonads is labile and gender is determined principally by environmental factors, often associated with density, and occurring at some early stage in the growth phase of the yellow eel. Based on microscopic and macroscopic observations, differentiation of the gonads occurs once the eels reach a threshold length rather than age, though this length threshold varies between individuals and populations.

SMEP II requires a description of the length at which an undifferentiated eel is expected to become male or female, and the probability of it becoming male or female under differing conditions of density. The user is required to define this mean length at differentiation, the shape of the curve describing how the proportion of females relates to density as a proportion of the local carrying capacity, and the density above which all undifferentiated eels become male.

4.3.1 Length at differentiation

It appears from the scientific literature that sexual differentiation is observable at lengths ranging from 100 to 400mm, although the range of values for individuals may vary considerably between populations and habitats. Examination of the maximum lengths of undifferentiated eels versus minimum lengths of clearly differentiated eels in the rivers of England and Wales studied by Bark *et al*. (2007) (Table 1), observations reported by Sinha and Jones (1967) for rivers in Wales, and the various studies of the Burrishoole system in Ireland (R. Poole, pers. comm.) suggests that differentiation is most likely to occur at lengths between 200 and 300mm. Given that mean values for the two groups in Table 1 are 213 and 187mm respectively, the default value for length-at-differentiation in SMEP II has been set at 200mm.

River	Max. length undiff. (mm)	Min. length diff. (mm)
Ellen	243	202
Wnion	217	103
Gara, Start	255	212
Darent	162	205
Colne, Blackwater (Essex)	211	195
Hull	197	184
Blyth	198	167
Mawddach	218	227

Table 1. Sexual differentiation in *Anguilla anguilla*, maximum lengths of undifferentiated eels and minimum lengths of sexually differentiated eels sampled from rivers in England and Wales during the Defra CTG0102 contract.

4.3.2 Relationship between sex ratio and site density (biomass)

Trends in the relative production of male versus female eels have been variously linked to differences in habitat, thermal regime, population density, growth rate and food availability, all of which may be interrelated to some extent.

Typically among eel species, males tend to predominate under conditions of high density (Roncarati *et al.*, 1997; Krueger and Oliveira, 1999; Walsh *et al.*, 2004; Han and Tzeng, 2006), which may be because a male ‘‘grow quickly, mature early’’ strategy increases an individual’s chances of survival during periods of intraspecific competition (Davey and Jellyman, 2005). Though overall growth rates tend to be faster in female yellow eels (for example see Melia *et al.*, 2006b), individuals experiencing rapid growth prior to gonad differentiation may be more inclined to develop as males, whereas eels that initially grow slowly are more likely to develop as females (Holmgren and Mosegaard, 1996; Holmgren *et al.*, 1997).

It has been shown that the relative proportions of fluvial versus lacustrine habitats within a basin can influence sex ratio of emigrating silver eels. American eels (*Anguilla rostrata*) migrating from lacustrine habitats within a river were predominantly female, while eels migrating from fluvial habitats were predominantly male (Oliveira *et al.*, 2001).

As noted above, a number of studies have suggested that conditions of high eel density favour a male-biased sex ratio. However, several factors make it difficult to quantify the relationship between sex ratio and density in order to describe and model this process at the reach or even individual scale, rather than for the whole river.

The absence of a non-destructive method of determining the sex of individuals means that it is very difficult to know when differentiation is initiated, and what environmental conditions result in an individual becoming male or female. Given that eels may spend more than 10 years in a river (and females could spend much longer than that), and could differentiate during the first few years, there might be a gap of several years (and opportunity for considerable movement) between the time when the eels differentiated and when density is measured at time of sampling. Thus, the conditions at the time of sampling might bear no resemblance to the conditions when differentiation to one or other gender was initiated.

Even in those fish most recently differentiated, or rather when gonadal differentiation has reached a recognisable stage, the driving conditions may have been several years prior to capture. Though gonadal differentiation has not been observed in eels at lengths less than 100mm (Bark, Knights and Williams, unpublished data), tank trials suggest that, under very high densities ($2kg.m^{-2}$) at least, gender may be ‘decided’ within four months of eels being caught as glass eels, even though gonads were not macroscopically differentiated for a further seven months (Huertas and Cerda, 2006). Studies that attempt to relate sex ratios to macroscopic habitat scales (such as whole river, lake, estuary or even basin) often ignore the possible variation in environmental regime experienced by the individual prior to capture.

Few studies have reported relationships between sex ratio and density within or between populations from which we can derive a model within SMEP II. Two studies relate elver recruitment to yellow or silver eel sex ratio. Rosell *et al.* (2005) linked the increase in the proportion of females in the silver eels emigrating from Lough Neagh, Northern Ireland, to a reduction in elver stocking rates since 1989. They suggest that elver stocking densities of 225 to 300 elvers per hectare (75 to $100g.ha^{-1}$) in this large, shallow lough resulted in a male-dominated population, and that densities lower than 150 elvers (50g) per hectare lead to a female-dominated population. Counts of upstream migrating elvers and downstream migrating silver eels in the River Imsa, Norway, during 1975 to 1987 (Vollestad and Jonsson, 1988) suggest that annual elver

recruitment ranging from 2457 to 48,615 (2 to 42 eels per hectare) resulted in silver eel output highly dominated by females (93-99 per cent). Note, however, that it is simplistic to relate elver recruitment to total wetted area and assume that the density-dependent influence on sex ratio occurs throughout the river area.

Few other studies consider yellow or silver eel sex ratio against yellow eel densities. Aprahamian (1988) measured densities in the River Severn in 1983 ranging from 500 eels per hectare (in the upper basin) to 32,000 eels per hectare (maximum value in the lower basin). All sites were dominated by female eels, with percentages exceeding 58 per cent. A decline in density from about 26 to 8 eels per 100m^2 (2600 to 800 eels per hectare) over 25 years in the River Piddle, Dorset, England coincided with a switch from male- to female-dominated eel populations (75 per cent to <30 per cent males) (Bark *et al.*, 2009). Similarly, Acou *et al.* (2009), reported a highly male-dominated (86 per cent) pre-migrant yellow eel population in the Fremur, France, where the overall yellow eel density was about 4000 eels per hectare, in comparison to a highly female-dominated (79 per cent) pre-migrant population in the neighbouring Oir, arising from a mean yellow eel density of about 300 eels per hectare.

Bark *et al.* (2007) also reported a significant negative relationship between mean density (measured across all sites: ~5 to 50 eels per 100m^2) and the proportion of female eels (~5 to 95 per cent) in their study of eel populations in 14 English and Welsh rivers. Though based on a relatively small sample size, their relationship had an r^2 of 0.656 and suggested rivers would be female-dominated at mean densities of less than 15 to 25 eels per 100m^2 (1500 to 2500 eels per hectare).

Reviewing some French, Spanish and Norwegian studies, Robinet *et al.* (2007) suggest some relationships between whole-river eel density and sex ratio of emigrating silver eels: rivers with mean densities, calculated across all sites, higher than 500-1000 eels per hectare produce mainly male silver eels (>90 per cent); whereas rivers with densities lower than 300 eels per hectare produce mostly female silver eels (>80 per cent). Thus, Robinet *et al.* suggest a density threshold of 500 to 1000 eels per hectare around which the sex ratio of silver eels swaps from being dominated by one to the other sex.

Although the UK results are not directly comparable with those of other European basins, since the UK studies refer to yellow eels whereas the others refer to silver eels, they do provide some information about the range of density values that can be associated with a considerable proportion of females in the population.

4.3.3 Sex ratios under extreme conditions: experimental studies

The information we have about the process of sex differentiation in eels is fragmented and sometimes contradictory. Because of the difficulties in studying this process in the wild, scientists have tried to study it in a controlled environment. Roncarati *et al.* (1997) reared elvers at densities of 800g per m^3, 1,600g per m^3 and 3,200g per m^3 - approximately 1,780 eels per m^3, 3,650 eels per m^3 and 7,200 eels per m^3. The three densities resulted in male to female ratios of 2:1 (33 per cent female), 3.5:1 (22 per cent female) and 25:1 (4 per cent female), respectively. Thus, even at densities much higher than those observed in English or Welsh rivers, a small proportion of undifferentiated eels still become females. As a consequence, the gender/density relationship in SMEP II will always result in at least five per cent female or male eels at extreme densities.

4.4 Mortality rates

Mortality is the loss of eels from the population, and can be due to a variety of factors, both natural (chiefly predation, diseases and parasites), and anthropogenic, both directly (due for example to fishing, turbines or scientific experiments) or indirectly (as a result of increasing density-dependent mortality due to greater densities below dams and weirs). There are few quantitative studies on mortality rates in eel populations because of the difficulty in actually measuring it via scientific methods (Knights *et al.*, 1996; Knights *et al.*, 2001). It is generally expected, however, that natural mortality declines as the length of individuals increases.

4.4.1 Natural mortality

SMEP represents natural mortality using a Weibull Distribution Model (after De Leo and Gatto, 1995), relating the probability of mortality to the length of the individual, with this probability decreasing as the eel grows in length. The user is required to define this function under average, minimum and maximum mortality conditions, and for stocked eels under the expectation that they will have a mortality rate that differs from local 'wild' fish, at least for some time after stocking.

Based on counts of recruiting elvers and emigrating silver eels in the River Imsa, Norway, Vollestad and Jonsson (1988) estimated an instantaneous rate of total mortality for on age cohorts from the 1970s and 1980s. It varied from 0.088 to 0.225 for the five year-classes studied, with an overall mean of 0.167. Rasmussen and Therkildsen (1979) observed mortality rates of 0.36 to 0.65 for eels from high density steams in Denmark, similar to the 0.56 to 0.66 in the Rio Esva, Spain (Lobon-Cervia *et al.*, 1995), though more recent studies under lower density conditions revealed rates as low as 0.099 (Lobon-Cervia and Iglesias, 2008). Dekker (2000) reports that 75 per cent of eel recruits die from natural causes, equivalent to an annual mortality rate of 0.1 to 0.2 over a lifespan of about 14 years.

As a consequence of our modelling approach, we ideally require measures of instantaneous mortality at different lengths or at least at stages (that is, glass eel, settled elver, undifferentiated yellow, differentiated yellow, silver); 'whole-life' studies of mortality do not provide the appropriate information. Natural mortality is assumed to be very high for the *leptocephalus* and the glass eel stages, based on consideration of the reproductive strategy of eels and their apparent high fecundity (0.5-3 million for 50-75cm eels and 5 million for 95cm eels) (Knights *et al.*, 2001). Knights *et al.* (2001) suggest stage-specific mortality levels of 99.99 per cent for oceanic larval stages, 90 per cent for the transition stage between immigrant glass eel and pigmented elver/early juvenile, and 75 per cent for the yellow eel stage up to emigration as a silver eel. In further study of the same population, Vollestad (1992) reported mortality of wild eels of length smaller than 15cm at 80 per cent per year. De Leo and Gatto (1996), using a process-driven model of eel from the Comacchio lagoons, Italy, estimated annual mortality rates of about 70 per cent for elvers, declining to 10 to 20 per cent for the oldest yellow eels (silvering at age 15 years).

It is assumed from general principles of fish biology that natural mortality will be influenced by density, but there is little information available to prove, let alone quantify, this relationship. Lobon-Cervia *et al.* (1995) found significant linear regressions between mortality/migration rates (which can be difficult to distinguish) and the initial numbers of eels for three of four tributaries of the Rio Esva, Spain. From a comparison of elver recruitment with silver eel escapement, Vollestad and Jonsson (1988) suggested that the survival rate of eels in the River Imsa was affected by density at glass eel recruitment levels greater than 20,000 per annum. This recruitment equates to a whole-river density of about 17 eels per hectare or 0.17 eels per 100 m^2, if we

were to assume that the recruits were evenly distributed throughout the productive area of the river. However, recruits are probably concentrated within a smaller area near the sea, and therefore the density threshold is probably higher, but no information is available regarding the wetted area over which density-dependent mortality occurs.

Survival rates of individual age 0 eels in the Comacchio lagoons was similar at high (3388 eels per hectare, 149kg per hectare) and low (597 eels per hectare, 55kg per hectare) densities, suggesting density-dependent mortality acting throughout this range (De Leo and Gatto, 1996) or no effect at all. Survival of age 1 and older eels, however, was negatively related to overall yellow eel density, which the authors suggested was due to varying competition for food and space, though noting that other environmental factors could not be discounted.

Given the difficulties in measuring natural mortality of eels *in situ*, it is hardly surprising that few studies have attempted this or even to explore whether it is the density of eels *per se* that matters or density of particular size classes that are utilising particular niches. The only such study we could find was that of Lobon-Cervia and Iglesias (2008), who reported a significant regression between cohort mortality rate and glass eel recruitment for eels of the Rio Esva, Spain, and an improved fit when the analysis included the density of accompanying cohorts. Few, if any, studies appear to have attempted to measure natural mortality of eels in relation to variation at the ecosystem level (such as density and so on of eel and other biota).

Because of the variation in the values found in the literature and the multiple factors that can affect eel survival, it is very difficult to choose appropriate values for survival at length. We have opted for mortality values that result in 70 per cent annual mortality at short lengths (to 200mm) which changes to above 30 per cent annual mortality for eels of length of 350mm or above. However, because the results of the model are very sensitive to the choice of these values, we would advise users to repeat their calculations with more than one set of mortality at length values, in order to have a good idea of the sensitivity of the results to using plausible (but different) sets of mortalities at length.

Tagging studies of silver eel migration in the River Meuse (The Netherlands) found that 37 per cent of eels reached the sea from tagging locations 260km upstream, typically travelling these distances in about 8 to 10 weeks (Winter *et al.*, 2006). Mortalities associated with hydropower and fisheries were each estimated to be 22 to 26 per cent, after accounting for unreported capture of tagged fish, and delayed mortality from turbines. Winter *et al.* (2006) attributed the remaining 11 per cent mortality to natural or experiment induced mortalities, tag loss or failure, and/or interrupted migration delayed beyond the end of the study, but could not further apportion mortality within this group. Adopting a worst case scenario, we can assume a natural mortality rate for silver eels during their downstream migration of 11 per cent. In the absence of similar study from other rivers, we have no evidence to suggest whether this rate would be lower for silver eels migrating over a shorter period or distance.

Natural mortality: predation

Neither SMEP nor SMEP II allows the facility to apply a predation-specific mortality to the modelled eel population. It is assumed, therefore, that predation will be incorporated with the natural mortality. However, it is briefly considered in this review as the control of predators was proposed as a potential management measure in the EU's Eel Regulation.

The impact of piscivorous birds was reviewed by the Working Group on Eels (WGEEL) in 2007 (ICES, 2007), who estimated that cormorant consumption of eel across Europe might be comparable with 30 to 50 per cent of the 1993/94 European eel commercial

fishing catch. Though mammalian and piscivorous predators of eel are known, nothing has been reported on their potential impact to eel production rates. If specific information is available, however, predation mortality can be simulated as if it were a fishery.

4.4.2 Anthropogenic mortality

Stocking

It is generally assumed that stocked eels will suffer a relatively high mortality compared to the naturally recruited eels in the stocked area, at least in the short term while the stocked fish acclimate to local conditions. Bisgaard and Pedersen (1991) used visible implants to tag wild and stocked eels (mean length 20cm at stocking) in a Danish stream. Based on recaptures after one year, they reported that the mortality rate of stocked eels (83.7 per cent) was much higher than that of the wild eels (59.9 per cent) in the same length range, though this difference might have been due, in part, to the greater tendency for stocked eels to migrate out of the study area.

Fishing

Fishing mortality is modelled in SMEP II as a loss from the population at one or more locations on one or more occasions, with the loss being described as the numbers of eels of a particular length range. SMEP II allows the user to describe this loss according to a variety of measures of fishing impact, ranging from numbers and lengths of individual eels in the catch, to a gear selectivity and fishing effort (= fishing mortality). At present (2010), commercial eel fisheries in England and Wales are required to submit annual catch returns to the Environment Agency. These returns should include information on the number of days fished per month, the location and type of water fished (river, coastal/estuary or still water), and the total weight of eels caught and retained per month. In accordance with the availability of such data, therefore, fishing mortality will most likely be defined for SMEP II based on the user defining the weight of the catch, the stage (glass, yellow, silver), the reach location, season and year.

Turbines

The mortality associated with downstream passage of eels through turbines is modelled in the same manner as a fishing event, assuming a user-defined percentage of silver eels are caught (killed) and that these are distributed across a defined length range. The model assumes that all turbine-related mortality is instantaneous. The European Inland Fisheries Advisory Commission (EIFAC)/ICES WGEEL recently reviewed studies on mortality levels from turbine passage, reporting rates ranging from 15 to 38 per cent (ICES, 2007).

Pollution

Mortalities associated with pollution events are not addressed by the model. The user could simulate a mortality associated with an acute pollution event, however, by defining a one-off mortality as for fishing. Chronic lethal effects of pollution could similarly be simulated as for fishing events. Sub-lethal effects of pollution are more difficult to model directly, but would be addressed indirectly in the parameters

describing growth and natural mortality; that is, growth might be slower and ‘natural’ mortality higher in a habitat where the eels were subject to long-term but sub-lethal pollution.

4.5 Maturation (silvering)

Within the context of SMEP II and its application, ‘maturation’ represents the transformation from yellow to silver eel stage, followed by the migration of the silver eels downstream out of the system and to the sea. As such, it might have been better described as ‘silvering’, since final maturation of the gonads might not occur until the fish approaches the spawning area.

The great variation in mean age versus mean length at silvering, and the fact that mean length at silvering does not appear to be affected by variation in growth rate, suggests that the process is triggered by critical length rather than age (Vollestad, 1992), whilst morphological changes during ‘silvering’ and downstream migration in any year are triggered by body condition, for example fat reserves (Svedang *et al.*, 1996; Jellyman, 2001).

Typically, males silver and emigrate at smaller lengths and younger ages than females, both in European eel and in other anguillid species (Vollestad, 1992; Tesch, 2003; Davey and Jellyman, 2005). The male eel strategy appears to be to reach maturity rapidly, at a small size and age range, perhaps almost as soon as their gonads are differentiated (Durif *et al.*, 2005; Bevacqua *et al.*, 2006). This may explain why male silver eels are produced primarily in productive areas such as estuaries and lower river areas, but are relatively scarce farther upstream in longer rivers (Walsh *et al.*, 2004). In long rivers, it could be that females are more inclined to move far upstream, and/or it could be that both sexes move upstream at similar rates but earlier maturing males emigrate before they reach the headwaters. Female age at maturity appears to be negatively related to growth rate, suggesting that the female reproductive tactic is to become sexually mature at a minimum size, dependent on a different set of threshold criteria (Svedang *et al.*, 1996).

In SMEP II, maturation (silvering) is represented by probability relationships, increasing with length above a threshold. The user defines the mean length and shape of probability function separately for males and females.

The lack of any substantial or systematic variation in mean length at silvering across populations of Europe and North Africa (Vollestad, 1992), means that single silvering-length functions for males and females can be used in applying the model to all UK eel populations. Tesch (2003), in reviewing published data on silver eel size from different rivers in Europe, found that silver male eels are typically of length 350 to 450mm and females greater than 450mm (means between 550 and 600mm). More specifically, silver eel trapped emigrating from the Burrishoole, Ireland, were 250 to 450mm for males and 400 to 650mm for females (Poole and Reynolds, 1996b), and Acou *et al.* (2009) reported male silver eel from the rivers Fremur and Oir, France, of lengths 300 to 437mm, and females of lengths 414 to 677mm.

For UK populations, male silver eels are typically of between 290 to 440mm, while female silver eels are between 350 and 810mm, but with few greater than 600mm (Aprahamian, 1988; Naismith and Knights, 1990).

Based on the information above it seems appropriate to assume that the most probable length values (that is, the mean of the probability distribution we use to describe this process) at which male eels will become silver lie in the range between 300 and

400mm (default 350mm) while the relevant values for females appear to be between 400 and 650mm (default 550mm).

As regards the shape of the curve describing the probability of an eel maturing (silvering) with increasing length, Bevacqua *et al.* (2006) presented cumulative silvering-at-length relationships based on yellow and silver eel fisheries of saline lagoons and a freshwater canal system in the Mediterranean regions of France and Italy. Both male and female relationships showed steep sigmoidal curves.

4.6 Movement of eels throughout a basin

The European eel makes extensive migrations at specific life history stages, with two oceanic and one continental phase. This report covers the movement of the eels during the continental phase, from their entrance into the study basin area to when they leave to spawn. For clarity, we refer to the downstream passage of silver eels as a 'migration', since this is clearly with the purpose of returning to the spawning grounds, whilst the less obligatory nature of their dispersal upstream through the basin is referred to as 'movements'.

SMEP II requires the user to define the tendency of eels to move from one to reach to a neighbouring reach (relative transition), the speed at which undifferentiated and differentiated eels travel (km per year).

4.6.1 Upstream movements

Although recent studies using otolith microchemistry techniques reveal that some proportion of eel populations spend their growth phase in saline waters (Tzeng *et al.*, 1997; Daverat *et al.*, 2004; Arai *et al.*, 2006; Daverat *et al.*, 2006), we focus here on the factors stimulating eels to move up from estuaries to freshwater, and to disperse throughout the freshwater habitat.

Water temperature seems to be the key stimulus controlling elver migration from estuaries into rivers, and there is a positive correlation between summer water temperatures and the numbers of eels ascending into freshwater (Hvidsten, 1985; Vollestad and Jonsson, 1988; Edeline *et al.*, 2006). Similarly, few small eels were trapped on rivers in England at temperatures below 10°C, and the numbers caught (which can be implied as the tendency to move) increased with temperatures above 15-16°C (Naismith and Knights, 1988; White and Knights, 1997).

The process of dispersal of yellow eels throughout freshwater basins appears to be driven by two mechanisms, corresponding to density dependent situations and an inherent tendency to move upstream. In UK rivers, Ibbotson *et al.* (2002) showed that density dependent influences on dispersal mainly apply to eels aged up to four years, whereas larger ones disperse randomly and slowly through the river basin. This tendency to slowly move upstream, coupled with the silvering of males at smaller length, results typically in a negative correlation between eel density and distance from the sea (Aprahamian, 1988; Naismith and Knights, 1990; 1993). The environmental and intrinsic factors involved in upstream movements change as eels grow, which determines the distribution of different size classes along the course of freshwater basins (Feunteun *et al.*, 2003).

Feunteun *et al.* (2003) proposed a general theory of upstream movement. 'Pioneer' elvers move upstream as far as they can, regardless of the availability of suitable habitats, whereas 'founders' move upstream until they find a suitable vacant habitat, and are typically driven by density-dependent factors. After these early movements,

which may occur over a few years, eels become either nomadic or home-range dwellers. Nomadic movements can be upstream or downstream, and include movements into estuaries and coastal waters. Home ranges can be as short as a few hundred metres (Bisgaard and Pederson, 1991; Baras *et al.*, 1998; Laffaille *et al.*, 2005).

Studies of eels in UK rivers suggest that yellow eels may move up to 46km in a year, but those eels that make significant upstream movements, travel on average around 10 to 30km in a year (Hussein, 1981; Moriarty, 1986; Aprahamian, 1988; Mann and Blackburn, 1991; Naismith and Knights, 1993).

Although a number of tracking and mark-recapture studies have been reported, the literature provides no direct measures of stage-specific rates at which eels disperse throughout river systems, let alone comparisons between rates at different densities. The ideal approach to collect such data would be a comprehensive tracking programme, marking eels soon after they enter the river system and repeat sampling throughout the system to provide information on distances travelled over time. However, such a programme would be very expensive, long term and of questionable transference between different river topographies (and has not, to date, been conducted). A pragmatic approach, therefore, is to derive dispersal rates from examination of the maximum distances upstream where eels of different length or age groups are observed during routine sampling programmes. Aprahamian (1988) adopted such an age-based approach in analysing his eel survey data for the rivers Severn and Dee, estimating average annual travel rates of 15-33km per year for age one eels, 10-20km per year to age four, and 5-21km per year for eight year olds. SMEP II requires length-based travel rates, however. Lasne and Lafaille (2008), used probabilistic modelling of the presence/absence of eel in the Loire basin, France and found that few if any eel less than 150mm occur at 100km+ from the sea, and few eels less than 300mm at 400km+ from the sea. Therefore, we explored the data collected by Bark *et al.* for the Defra Project (CTG0102) and the Severn and Dee data provided by Aprahamian (1988) to investigate rates of travel for undifferentiated eel of two length-classes in rivers of England and Wales.

Distance from each site to the estuary was estimated using GIS maps (Environment Agency) to provide the distances that eels of various length classes were found above the tidal limit. SMEP II requires user-defined dispersal (movement) rates for undifferentiated and differentiated eels, with an associated, user-defined length at differentiation. We examined the travel rates of eels less than 100mm in length, in anticipation that these elvers may disperse at a faster rate than larger yellow eels, and those of undifferentiated eels between 100 and 200mm in length.

Initial consideration of the available data and the characteristics of the rivers and their eel populations revealed issues regarding the impact of instream structures (partial barriers) and areas beyond which small eels seem reluctant/unable to move. The dispersal of elvers (<100mm) in the River Blyth was limited by a dam 5km from the estuary, but undifferentiated eels (<200mm) were found throughout the 30km river length from sea to source. None of the survey sites in the Rivers Darent or Colne produced elvers, and undifferentiated eels were only found in the sites within 15km of the estuary. These rivers have tidal barrages, which appear to affect the upstream migration of elvers. The River Hull also has a tidal barrage, and none of the sampled sites had elvers, whilst undifferentiated eels were rare across all sites. Where physical constraints such as barriers clearly impede upstream movement of elvers, the data from these rivers are not suitable for deriving standard or potential dispersal rates for such small eels.

Few elvers were detected in the River Piddle, but recruitment to this river is thought to be dominated by older eels moving up from Poole Harbour in which recruiting elvers

seem to remain (Mann and Blackburn, 1991; Bark *et al.*, 2009). Undifferentiated eels were observed up to 20km from the estuary.

Three other rivers were excluded because they were very short. The Blackwater sites were all within 10km of the estuary and no elvers were captured. The sites on the Rivers Gara and Start were all within 15km of Slapton Ley (a natural impoundment adjacent to the sea), but elvers and undifferentiated eels were found throughout the 10-15 km of these tributaries. As these sites are all well within the range of distances over which elvers had migrated in other rivers, it was concluded that these data were not suitable for our analyses.

After excluding these rivers, we were left with data from four rivers. In the River Ellen (average gradient 1.6 percent), elvers were found up to 20km from tidal limit, and undifferentiated eels were found at the top site, nearly 40km from the tidal limit. Similarly, in the Wnion (gradient 2.5 per cent), elvers were found up to 15km from the tidal limit whereas undifferentiated eels were found up to 27km from the tidal limit. In comparison with these short and steeper rivers, elvers were detected in the River Severn (gradient <0.1 per cent) at least 80km upstream from the tidal limit, and undifferentiated eels to at least to 110km. In the River Dee, elvers were detected up to 50km from tidal limit (Chester Weir), and undifferentiated eels at up to 76km from the tidal limit. Thus we have comparisons between steep and shallow gradient rivers. Both the Severn and Dee have a number of weirs, etc that may slow the upstream migration of young eels, so the potential migration rates of young eels in shallow gradient rivers without obstacles may be faster than estimated from these data.

As SMEP II uses information on the distance that the eel can travel per unit of time (time-step), we are required to convert distance-at-length from survey data to age(time)-related travel rates. However, the broad range of lengths for eels at each age prevents us from using a simple length-at-age key based on single years, hence our use of the stage- and length-based classes. Furthermore, given the wide overlap of lengths of eels at age, it is not appropriate to estimate travel rates based on a mean or median age, so the analysis is limited to considering the minimum and maximum speeds of travel by two size classes within the undifferentiated stage.

The age structures of the two length classes are based on the length-at-age of Severn eels: eels less than 100mm ('elvers') in length ranged from 0 to 4 years, and undifferentiated eels (100-200mm) range from 1 to 14 years. Based on these age ranges, the travel rate of elvers in the Ellen (steep gradient) might be between 5 and 20km per year, whereas comparable rates in the Severn and Dee (shallow gradient) would be 25 to 80km per year, and 12.5 to 50km per year respectively. Since undifferentiated eels were found throughout the Ellen, the minimum travel rate was 2.9km per year, but the maximum rate could not be inferred from these data. The minimum rates for undifferentiated eels in the Severn and Dee were 7.9 and 5.4km per year, respectively, whereas maximum rates are 125 and 76km. This variety in speed of travel provides a range of values that can be applied in SMEP when one is considering various scenarios. In the first instance, however, we suggest a default rate for undifferentiated eels in steep gradient rivers of 10km, falling to 5km per year in differentiated eels, and 30km for undifferentiated eels in shallow gradient rivers, falling to 10km in differentiated eels.

4.6.2 Downstream migrations of silver eels

As with upstream movement, temperature seems to be one of the main cues to initiate downstream migration in silver eels, although length of day, high water flows and increased water levels (from increased precipitation) are also implicated (Vollestad *et al.*, 1994; Feunteun *et al.*, 2000; Cullen and McCarthy, 2003). Little is known, however,

of the speeds of silver eels in freshwater when measured from the position that they start their migration to entry into seawater. Though tagging studies of silver eel migration in the River Meuse and Rhine, Germany, indicated that eels could travel up to 350km from tagging location to the sea in about 8 to 10 weeks during the autumn (Winter *et al.*, 2006; Klein Breteler *et al.*, 2007), the vast majority of rivers in England and Wales are considerably shorter and have different characteristics.

Some studies have reported an interrupted migration, whereby silver eels delay completing emigration for periods of weeks or even years (Vollestad *et al.*, 1994; Feunteun, 2002; Westin, 2003; Winter *et al.*, 2006). There are doubts, however, as to whether this behaviour might be an artefact of the study method (Winter *et al.*, 2005) or, indeed, whether the study animals were fully 'committed' to their emigration (Feunteun *et al.*, 2000). Several studies have suggested using morphological indicators of silvering status in eels (Acou *et al.*, 2005; Durif *et al.*, 2005), but variations between morphology of eels from the same and different rivers casts some doubt on the universal utility of these indicators.

Given that few eel-producing habitats in England and Wales are more than 300km from the sea, we have assumed that eels from all our rivers ought to be able to emigrate to the sea in the season (August to December) during which they become silver.

4.7 Quality of habitats and carrying capacity or productive potential

The effect of different habitat types on the various life processes of eel is an important factor in the application of SMEP II, and has been considered in the relevant sections above. What remains here is a review of the relative productive potential of different habitats, which could be used to 'inform' the model application according to some indices of habitat quality. Production may be influenced by direct mechanisms on the processes and the eel population, or by indirect mechanisms acting on the inputs to the population (that is, recruitment) by virtue of the location and physical characteristics of the habitat.

The carrying capacity of a system, whether it be a river reach, an estuary or a river basin, can be expressed as the maximum density or biomass of eels that the habitat can sustain under average conditions (in the medium term; that is 10 to 30 years). This can be linked to the productivity of a water body, with the more productive habitats having a higher carrying capacity that sustains a greater biomass. In a heterogeneous river system, the resources are clumped or unevenly distributed, such that the carrying capacity of any area (such as survey site or reach) may be limited by the availability of suitable habitat and food resources, which in turn may depend on eel size (Lobon-Cervia *et al.*, 1995).

The majority of published studies describe how habitat preferences change with the sex and size of specific eels. As discussed above, in relation to the exploration of any relationship between density and sex ratios of yellow eels, we must remember that the character of the observed local eel population may be influenced by factors that occurred at another place or time (or both). It may be very difficult, therefore, to conduct reach-based analyses of apparent habitat-life history relationships, and it may be more appropriate to consider differences at the whole river or basin scale.

An ICES report (2006) on the current status of the European eel covers this topic succinctly. It states that 'trophic' status (that is, oligotrophic, mesotrophic, eutrophic, hypereutrophic) should provide an approximate guide to potential carrying capacity. Bark *et al.* (2007) observed that English and Welsh rivers with relatively high nitrate levels are associated with higher eel growth rates. Based on data from rivers that they

considered were at or close to their productive potential (that is, where recruitment was not thought to be not limiting), they reported a highly significant positive relationship between nitrate levels (Ni) and maximum standing-stock biomass of eel populations. [$Bmax = 0.019Ni^2 + 0.110Ni + 2.546$, where *Bmax* is in $g.m^{-2}$ and Ni is $mg.l^{-1}$] The presumed maximum eel biomasses (*sensu* carrying capacity) ranged from about 500 to 2500g per100m^2, from waters with nitrate concentrations ranging from about 2 to 34mg per litre.

In order for SMEP II to model density-dependent effects, the user is required to define a biomass threshold (in g per 100m^2). This is treated by the model as the threshold biomass above which the density-dependent effects have their maximum effect. Note that it is not the maximum biomass that can be produced in any reach.

Eel distribution, density and population structure in a particular catchment is primarily dependent on the annual recruitment of elvers to the estuary, the number subsequently migrating into freshwater, and the numbers moving upstream, which is strongly influenced by the presence of barriers to migration (Naismith and Knights, 1993). Given the decline in recruitment observed at the European stock level, and probably between 70 and 95 per cent in English and Welsh rivers, eel production may be significantly lower than potential productive capacity in all but a few rivers in England and Wales, and even then only in the reaches closest to estuaries in these rivers. Therefore, population biomass data from the period prior to the recent decline in recruitment (that is, before the early 1980s) may be the most appropriate indication of potential productive capacity of rivers in England and Wales (assuming that water quality has remained stable since then, which is not necessarily the case).

Biomass data from eel-specific surveys conducted in the Piddle/Frome, Severn and Dee catchments during the 1980s showed maximum site biomasses ranging from about 2,200 to 5,800g per 100m^2. Maximum site biomasses from these and 12 other river systems in England and Wales between 2002 and 2004 ranged from ~1,000 to 5,300g per 100m^2 (Aprahamian, 1986; Aprahamian, 1988; Mann and Blackburn, 1991; Bark *et al.*, 2007). Maximum site biomasses reported for Scottish rivers are around 3,400g per 100m^2 (Carss *et al.*, 1999).

4.8 Quantitative estimates of silver eel production

The aim of this section is to identify silver eel production values with which we could compare with the model outputs to ensure the model is providing reasonable values. The EIFAC/ICES WGEEL (2008) reviewed estimates of silver eel escapement (production) for different habitats across Europe, and summarised these for the periods pre- and post-1980 to reflect periods of relatively high and low recruitment. The results were further compared according to the dominant productive environment; that is, lakes, rivers, lagoons and marsh habitats.

There are few studies of silver eel production before 1980. Riverine systems produced about 1.9 to 49kg per hectare (n=4), whereas systems dominated by lakes (>50 per cent wetted area) produced 0.3 to 17.4kg per hectare (n=4). Production from marsh and lagoon habitats was 43.7 and 20kg per hectare respectively, though there was only one estimate for each.

From 1980 onwards, there have been more studies of silver eel production rates (ICES, 2008 reported 50), but the data are by no means comprehensive given the wide variety in geographic, physical and biological factors influencing eels in across their range. Furthermore, there has been a general decrease in glass eel recruitment during this period, which will have limited silver eel production. As a consequence, recently measured/observed production rates may be lower than their potential maximum.

Countering this, many of the studied lakes have eel populations that are supported by stocking and would have been buffered from the recruitment decline to some extent. Estimates of silver eel escapement from rivers ranged from 2.7 to 16.4kg per hectare (n=3), from 0.2 to 6.4kg per hectare for basins dominated by lakes (n=4), from 0.04 to 4.4kg per hectare from lakes (n=35), and from 6.2 to 30kg per hectare for lagoons.

4.9 Recruitment /settlement

A measure of recruitment of eels to the study river is required where a simulation occurs over a number of years. It is important for the user to recognise that 'recruitment' here is the income of eels to the study area, and not necessarily the amount of glass eel entering an estuary. Of course, if the study area includes an estuary, then recruitment will mean the amount of glass eel entering the estuary from the sea. If recruitment information is available, the user is required to define it as the annual number (millions), the mean length of recruits (mm) and the standard variation (mm) about that mean.

There are very few examples of measured recruitment. Glass eel recruitment to the River Bann estuary, Northern Ireland, ranged from about 10 million to 30 million during 1933 to 1947, from 6 million to 27 million during 1960 to 1974 (Parsons *et al.*, 1977), and has apparently declined from around 11 million to 4 million since the late 1980s/early 1990s (M. McCauley, pers. comm.; Rosell *et al.*, 2005). In comparison, the catch of the Vilaine glass eel fishery, France, during 1995 to 2000 suggests a minimum glass eel recruitment of 42 million to 69 million (Briand *et al.*, 2003). However, these may not be appropriate reference points for our modelling requirements, since we are simulating recruitment to the river basin population and subsequent production, rather than glass eel recruitment to coastal waters or estuaries. The latter will be subject to large and possibly variable levels of mortality, which are not included in the model. To avoid confusion of terms therefore, we use the term 'settlement' when considering the effective influx of eels to the study population.

Given the lack of historic or present-day measures of settlement in any study area, this will probably most often be inferred by backwards projection from numbers of small yellow eels observed in surveys or fishery catches.

Trends in recruitment/settlement are required if the user wants to model backwards to estimate production under 'pristine' conditions, or forwards to model production on the basis of management changes. As the eel is a panmictic stock, the historic trend in recruitment is usually derived from the pooling of glass eel abundance indices from across Europe. This analysis is conducted and reported by the WGEEL every year. There is considerable variation in trends between river indices, however, and it is probably more appropriate to apply a UK trend when modelling UK eel populations.

There are no fishery-independent time series of glass eel recruitment or settlement in UK rivers, and therefore catch returns for commercial fisheries are the only means of assessing trends in recruitment (Bark *et al.*, 2009). Comparison of reported catch with estimates of nett export from HMRC records suggest, however, a high level of under-reporting of catches, and that this level varies between years. Variation in annual catches can reflect changes in fishing effort as well as in 'stock' abundance, and we should examine trends in catch standardised according to effort; that is, catch per unit effort (CPUE). In the absence of information on the actual fishing effort associated with these catch returns, CPUE can only be estimated according to the number of eel fishing licences sold by the Environment Agency and its predecessors. Despite these concerns about the quality of the CPUE data, these are the only data from which to assess trends in recruitment (Walker *et al.*, 2009).

In the absence of direct measures of recruitment to a study area, changes in yellow eel population structure (such as numbers, biomass, length distribution) over time can provide a proxy indication of trends in recruitment. Data for historical surveys of eels in UK rivers are limited, however, and time series comparisons do not suggest consistent patterns. Bark *et al.* (2009) found no consistent trends in mean yellow eel density, biomass and cumulative length-frequency of eel populations from survey sites in the lower Severn basin between the early 1980s (after Aprahamian, 1986), late 1990s and early 2000s. Upper basin surveys were not repeated in the 1990s or 2000s, but the authors concluded that the continued wide distribution of eel throughout the upper reaches of the Severn suggested that any decline in glass eel recruitment had not significantly affected the freshwater population in this basin. In contrast, the eel population in the Rivers Piddle and Frome, which share a common estuary, display considerable declines in both numbers and biomass of eel at survey sites (~60-70 per cent). Together with significant shifts towards larger eel dominance in length frequency distributions, this strongly suggests major recruitment declines in recruitment between the late 1970s and the early 2000s (Bark *et al.*, 2009).

Consideration of these geographic patterns, and recent (2002-2004) surveys from 14 other rivers around England and Wales, led Bark *et al.* (2007) to suggest that recruitment to estuaries and rivers in the west and north east of England and Wales remains high enough to maintain local stocks close to their productive potential, unless there are structures that hinder the upstream dispersal of small eels. In contrast, rivers in the eastern and south eastern regions may be far below their productive potential due to low recruitment (noting the ‘shadowing’ effect on continental immigration). Of course, this presupposes that historic recruitment to eastern areas was high enough to allow for a productive potential similar to western areas, but anecdotal evidence of recent declines in fishery catches from the Norfolk Broads (M. Pawson, pers. comm.) and from Anglian river survey data (Environment Agency, Ros Wright, pers. comm) provides support for this argument.

5 Application of the model (user guide)

This chapter can be considered as a comprehensive user guide to the application of SMEP II. The chapter is set out such that it first takes the user through the data files and options necessary to run the model. It then illustrates the potential application of SMEP II to address the requirements of the Environment Agency in assessing and managing eel stocks: setting the long-term management target; estimating the present-day and future escapement; setting intermediate (proxy) indicators; and identifying and prioritising management options available to increase escapement.

It is anticipated that some users may refer only to this user guide when applying the model. Therefore, though fully discussed in Chapters 3 and 4, some details of the manner in which SMEP II characterises life history processes, and the associated data requirements, are repeated here in order to provide a 'stand-alone' guide.

The input and model output files are all contained within a specific folder structure, which must be conserved in order for SMEP II to be able to access the appropriate files and information. Therefore, we strongly advise that a new copy of the folder structure is constructed for each model application. To aid the user in their identification, input and output files are highlighted in bold text, whereas options within input files are shown in italics.

5.1 Parameterising and running the model

In order to run a simulation, SMEP II must at least access information describing the scenario settings, the eel life history processes and the river basin in question. This information is supplied in three user-input files: the **First-File.csv**; **Parameters.csv**; and **Reach_Definitions.csv**. This information is the minimum required in order for the model to predict potential escapement under 'pristine', constant conditions, if no information was available on the status of the local eel stock under such conditions.

Where data are available, either for historic or present conditions, these can also be applied to characterise the yellow eel population (in the past or present), impacts on escapement (such as fishing or turbines), inputs such as stocking events, and changes in the available area and quality of habitat. These additional data allow the user to set the model to simulate escapement under various conditions (past, present and future), and to alter the effects of impacts and inputs in order to examine their relative influence on escapement.

5.1.1 First_File and associated files

The model conditions are set in the **First_File.csv**. Here, the user sets the length class structure of the simulated population; the number of reaches in the river network; the number of years in the simulation; whether or not the population starts in equilibrium, and the number of years to run the simulation to establish equilibrium. The user also

specifies which external factors are to be simulated (such as recruitment trends, fishing impacts, stocking and/or variations in habitat quality).

If a constant level of annual recruitment is selected (option 0), then the model will use the number of recruits specified in the **Parameters.csv** file. However, the user could select option 1 or 2, which vary the proportion of recruitment in relation to observed trends in UK recruitment levels, or option 3 that allows them to specify river-specific recruitment during the time series simulation. In the case of options 1 to 3, the recruitment trend must be specified in the **RecruitmentLevels.csv** file. The declining trend in UK recruitment from 1980 to 2010 is supplied as a default, along with the trend reversed to simulate recruitment recovery. The data used to construct these trends are the annual glass eel catch reported to the Environment Agency, relative to the number of licenses sold each year (that is, catch per unit effort: CPUE) (Walker *et al*., 2010). The annual data are indexed against the average CPUE for 1980 to 1982, which were the three years of data prior to the significant decline starting in 1983. The declining trend is provided in the **UKRecruitment.csv** file and the reverse trend is provided in the **ReverseUKRecruitment.csv** file, both of which are provided in the **Pre-defined** folder.

The user can specify whether fishing will be used in the calculations and the type of information that will be provided to describe this process. If the user chooses '0' for this option the model automatically assumes no fishing activities take place. If the user chooses either option 1 or 2, fishing is included. The user then needs to describe the fishery impact either as catch by length for option 1 or catch by stage for option 2. The names of the two optional input files are **TotalCatchByLength.csv** and **TotalCatchByStage.csv**, respectively. These data and the file are described in more detail below.

Similarly, if stocking is to be simulated (option 1), this is described in terms of the number and length distribution (mean length and range) of stocked eels, the reach where they are stocked, and the season and year when the stocking takes place. The user provides this information in the **Stocking.csv** file.

Variations in habitat quality are characterised in terms of their relative impact on the maximum biomass of eel that each reach can sustain. If the user selects the constant habitat condition (option 0) then all reaches will be able to sustain the same area-specific biomass of eel (that is, g per 100 m^2), which is specified as '*MaxBDensity*' in the **Parameters.csv** file. However, the user can elect to specify reduced potential biomasses for reaches where less-than-ideal habitat quality is thought to impact on potential production of eel (option 1). In this case, the user assigns a value for each reach proportional to the habitat quality impact in the **EnvHabScores.csv** file (that is, 0-0.99).

Note that the impact of in-stream structures (barriers) is not considered in the **First_File.csv**, but is specified in the **ReachPositioning.csv** file as part of suite of files describing the water network. These files are described later in this chapter.

Set_the_main_assumptions_for_the_model	Choices
Is_it_Deterministic_(D)_or_Stochastic_(S)?	D
Will_it_use_observed_data?_(Y_or_N)_(only_in_deterministic_mode)	N
FOR STOCHASTIC SIMULATIONS	
Do_you_want_a_Fixed_(F)_or_Random_(R)_seed?	F
How_many_simulations_are_required?	1
SET MAIN MODEL STRUCTURE	
What_is_ the_maximum_length_of_eels_(in_mm)?	1000
What_length_class_(mm)_is_used?	10
How_many_reaches_in_the_river_network?	15
How_many_years_should_the_model_project_forwards?	80
INITIALISATION OF POPULATION	
Does_the_population_start_in_theoretical_equilibrium_or_known_state?	3
The_equilibrium_simulation_will_run_for_how_many_years?	200
EXTERNAL FACTORS	
What_is_the_recruitment_pattern?	3
How_will_fishing_be_represented?	0
What_environmental_conditions_will_apply?	2
Wiil_stocking_be_included?	0

Figure 5.1. Example configuration of the First_File.csv.

5.1.2 Parameters and associated files

The **Parameters.csv** file allows the user to define the biological processes that apply to the life cycle of eels in the study river (such as growth, sex differentiation, natural mortality and silvering). A series of default parameters are provided for scenarios where there are no river basin-specific eel data to characterise some or all of these processes. These default parameters have been selected to represent average or typical values for eels found in river networks of England and Wales (see Chapter 4 for more details).

The first option in this file is the default time step (years) over which the model applies all these processes. The default is a three-month time step – winter, spring, summer and autumn – and therefore applies the processes and updates the simulated population every three months. The model has been specifically constructed to operate on this basis, and we strongly advise against changing this time step, as changes might result in some processes being wrongly applied.

SMEP II offers three different forms of growth function (linear, von Bertalanffy or Schnute). The user selects the growth function appropriate to the available data and defines the relevant parameters – all lengths are provided and modelled in millimetres. Only one form of growth function can be used in any one run of simulations, but the user can define different model parameters for undifferentiated, male and female eels where appropriate. The model applies growth during the third time step each year (summer).

Although the concept of a habitat having a carrying capacity for eel is accepted in theory, the quantification of that capacity is complex (see Chapter 4). Nevertheless, the model requires a limit density of eels on which to base density-dependent functions of sex differentiation, natural mortality and movements. Therefore, the user is required to specify a habitat capacity threshold (*MaxBDensity*) in terms of a density biomass of eels per unit area ($100m^2$). The default value is the maximum biomass of eel observed in eel-specific electrofishing surveys of lower tributaries of the River Severn in 1983 (Aprahamian, 1986), which are assumed to reflect natural high densities prior to the subsequent recruitment collapse.

The maximum number of recruits (millions) to enter the study system in any year is specified as the '*MeanRecruits*' value. This is the number that the model uses if the user selects the constant recruitment option in the **FirstFile.csv**, and to set the level for maximum recruitment if the user selects the option to use trends of recruitment. Recruits are also characterised by their size, with the user required to provide the mean and spread of lengths. Note that recruitment does not necessarily only refer to glass eels, but can be set to include larger eels where necessary, for example where the study wetted area starts above an estuary, lagoon or lake that acts as a 'sink' for small eel, or where the study wetted area is a tributary within a large river network.

Sex differentiation is characterised by the average length (mm) at which differentiation occurs (*DiffLength*), the shape of the relationship between density and the probability of becoming male, and the proportion of 'observed' density relative to the *MaxBDensity* threshold above which all undifferentiated eels become male (*UndiffSatLevel*). The relationship between density and sex ratio is adapted from that of Bark *et al.* (2007) and we advise against changing this unless new data become available.

In the case where the user wishes to model a population where the density and length distribution of eels is known but the sex ratio is unknown, SMEP II will assign all the eels under 200mm as being undifferentiated. As most emigrating silver male eels in UK are less than 450mm, SMEP II will assign all eels larger than this as females. The user can alter this all-female threshold (*lengthAllFemale*) if required. Finally, the model will assign the eels between the differentiation and all-female thresholds as being males or females according to the density-proportion of males ratio set by the user.

The model can simulate the effects of natural mortality in two ways, using a Weibull function to describe mortality-at-length (see Chapter 3 for full description), or using mortality values specified for each length class. The latter are provided in the **Mortality.csv** optional input file.

The probability of male and female eels silvering is described by two sigmoidal functions of fish length, with parameters setting the steepness (*MatCurveF, MatCurveM*) of the curve and the mid-point inflection in mm (*MatInflectionF, MatInflectionM*). The default values are based on length distributions of silver eels from four rivers across England and Wales.

Although SMEP II is an age-, and length-based model, the threshold densities are set as biomass and, given that the EMP target is a biomass of silver eels, it is necessary for the model to convert eels at length to weight. An allometric length-weight function has been derived from data for over 16,000 eels collected throughout England and Wales (Aprahamian, 1986; Aprahamian, 1988; Aprahamian, 2000; Knights *et al*., 2001; Bark *et al*., 2007; and unpublished Environment Agency and Cefas data).

The original model, SMEP, included a function to calculate the potential fecundity of female silver eels, expressed as millions of eggs. Although the fecundity of artificially matured female silver eels has been measured, the actual fecundity of mature silver eels has never been measured on the spawning grounds, and we have no knowledge of what proportion of immature eggs mature and are spawned. Therefore, we chose to remove the fecundity information from the input and output files of SMEP II. However,

although the relevant calculations have been disabled in the programme code, they have not been deleted in order to allow some degree of future proofing in case our knowledge of putative fecundity in the wild improves.

The speeds at which undifferentiated, yellow and silver eels move throughout the river basin are specified as kilometres travelled per year (such as e.g. *MaxUndiffMovementRate*). The default values are derived from the distribution of aged eels from the surveys of Bark *et al*. (2007) expressed in terms of kilometres from the tidal influence. It is possible that yellow eels move both upstream and downstream, but studies suggest that the tendency is overwhelmingly in the upstream direction (Ibbotson *et al*., 2002; Feunteun *et al.,* 2003) and therefore SMEP II allows yellow eels to move upstream only. It is assumed that silver eels only move downstream and so this direction has been fixed in the model. The user can vary the sensitivity of the eel movement (that is, the proportion moving) to the relative saturation levels of eels in neighbouring reaches (*RelativeTransition*).

Eel life history process parameters:	Value:		Eel life history process parameters:	Value:
default_timestep	0.25		CARRYING CAPACITY / ENV QUALITY:	
			MaxBDensity	2600
GROWTH:			CurrentEnvHabIndex	1
choice_of_model	1			
GrowthSeason	3		RECRUITMENT:	
GrowthTimeStep	1		MeanRecruits	10
			CVMeanRecruits	0.005
SCHNUTE GROWTH MODEL -FEMALES			MeanLength	60
length_minF	0		SDLength	20
tau_minF	0		MinRecLength	40
length_maxF	895		MaxRecLength	100
tau_maxF	1.00E+15			
kF	5.72E-02		SEXUAL DIFFERENTIATION:	
gammaF	1.00E+00		DiffLength	200
SCHNUTE GROWTH MODEL -MALES			UndiffSatLevel	0.95
length_minM	0		lengthAllFemale	450
tau_minM	0.00E+00		OgiveType	1
length_maxM	363		SDinflection	0.5
tau_maxM	1.00E+15		Diff_range	0.45
kM	1.09E-01		Sdpower	1.2
gammaM	1		SDslope	1
SCHNUTE GROWTH MODEL -UNDIFFERENTIATED				
length_minU	0		NATURAL MORTALITY:	
tau_minU	0		InputMortality	0
length_maxU	363		NMgamma	0.15
tau_maxU	1.00E+15		NMgammaMax	0.3
kU	1.09E-01		NMgammaMin	0.15
gammaU	1		RestockingMortality	0.2
VBF GROWTH MODEL _FEMALES			SILVERING:	
vbf_LmaxF	9.50E+02		MatCurveF	2.58E-02
vbf_kF	5.00E-01		MatInflectionF	550
VBF GROWTH MODEL _MALES			MatCurveM	6.40E-02
vbf_LmaxM	9.50E+02		MatInflectionM	350
vbf_kM	2.00E+01			
VBF GROWTH MODEL _UNDIFFERENTIATED			LENGTH-WEIGHT:	
vbf_LmaxU	950		LWalpha	5.42E-07
vbf_kU	0.5		LWbeta	3.196
LINEAR MODEL - FEMALES			MOVEMENT:	
growth_slopeF	2.00E+01		RelativeTransition	2
			MaxUndiffMovementRate	120
LINEAR MODEL - MALES			MaxYellowMovementRate	5
growth_slopeM	20		MaxSilverMovementRate	10
LINEAR MODEL - UNDIFFERENTIATED				
growth_slopeU	20			

Figure 5.2. Example configuration of the Parameters.csv file. Note that the process parameters are coloured here (the .csv file format does not support coloured fonts) to indicate those that the user could consider varying (green), those that are unlikely to vary except if robust local eel data are available (amber), and those that we strongly advise against changing (red).

The values provided in the **Parameters.csv** file reflect our understanding of the life history of eels in the UK (see Chapter 4). The user is able to change any of these parameter values, where knowledge of the local eel population provides a more appropriate value. However, we strongly recommend against uninformed changes, with three exceptions.

First, the user will almost certainly want to vary the amount of annual recruitment, in order to explore maximum potential production from the river network. Second, the user may have access to growth data for the specific river basin. Third, our

understanding of natural mortality process is particularly limited and the user might wish to explore scenarios built on maximum and minimum rates of mortality.

5.1.3 Reach definitions and associated files

Describe the spatial structure of the study basin

The Eel Regulation requires that each EMP should be based on River Basin Districts that constitute natural habitats for the European eel and which include coastal lagoons, estuaries, rivers and communicating inland waters (such as lakes, reservoirs, dykes and canals). At present, the Environment Agency has defined the outer limit of estuaries to be a straight line between headlands, but these reference locations are less discrete for some estuaries (such as the Severn) and this definition requires further consideration, perhaps with reference to habitat definitions of the Water Framework Directive.

The spatial aspect of SMEP II (that is, density-dependent effects on various eel life-history processes) requires a user-defined description of all the reaches. The ESRI® Arc-GIS-based RiverReach tool allows the user to construct the **ReachDefinitions.csv** and **ReachPositioning.csv** files to provide the relevant input data. The RiverReach tool has a comprehensive user guide, including step-by-step protocols for installing the tool, for defining reaches from GIS maps (in terms of their order, length, wetted area and connectivity between reaches) and specifying the locations and impacts of in-stream structures which might pose an obstacle to eel movement. This user guide is provided as an annex to this report, but the protocol is summarised here to illustrate the types of data required for the model application.

The user starts with an ESRI-format GIS map of the river basin. Cefas used the Environment Agency-CEH river network dataset (DEM) during the model development, but the protocol should be the same with the new Detailed River Network (DRN). The user locates points on the riverline to create reach boundaries, and the tool automatically calculates the length and wetted area of each reach.

How many reaches?

SMEP II uses reaches to control the area-dependent production of eels and to determine the relative impact of mortalities and stocking on the whole catchment production of eel. For example, a silver eel fishery or turbine 100km from the sea can only impact on the silver eels produced in reaches upstream of this location.

Although the new user may be inclined to insert reach boundaries at every intersection between two tributaries, in fact there is little to be gained in having more reaches than necessary, given the limited distribution of eel survey data, impacts (mortalities), inputs (stocking) and variations in habitat quality (river, lake, estuary; relative to ideal). The construction of the reach files and associated eel data input files is probably the longest task in the model application, and the more reaches defined, the longer this task will take (without necessarily improving precision). In particular, when defining the reaches for modelling based on an observed (surveyed) stock of eels, the user is required to input eel data for every reach (described below). As resource limits mean it is highly unlikely that survey data will be available for more than a few sites throughout the river basin, the user needs to extrapolate the survey data across the nearby productive areas. There may be nothing to be gained from extrapolating to ‘empty’ reaches compared to combining ‘empty’ reaches into a single, larger reach. The exceptions are

where it is necessary to model a discrete impact at a particular location in the river network, for example a silver eel fishery or a barrier causing mortality.

There is no rule for choosing the locations of reaches, but we recommend the following:

- Reach boundaries should be placed at significant in-stream obstructions and/or sources of mortality such as fisheries or turbines, 'significant' being those for which the user will vary the associated impacts in order to test different scenarios.
- Reaches should contain single survey locations, fisheries, other mortalities or stockings. SMEP II cannot use more than one set of descriptive data per reach – if there are two or more datasets then the user has to combine the data in some way, though we note that with respect to sampling sites, it is much better to have populations well sampled and to combine data within a reach as necessary.
- The only purpose in having 'empty' reaches (that is, with no survey, fishery, stocking or in stream structures) is 1) where two or more significant tributaries join the river within the reach, or 2) where an area of habitat is currently unavailable to eels but may be opened under some management scenarios.

As part of the reach definition process, the user assigns a unique code to each reach. The reach at the downstream end of the river basin is always labelled Reach 1, and reaches upstream should be labelled sequentially in order of their increasing distance from Reach 1. The tool has an option for showing the reach labels on the map (Figure 5.3.).

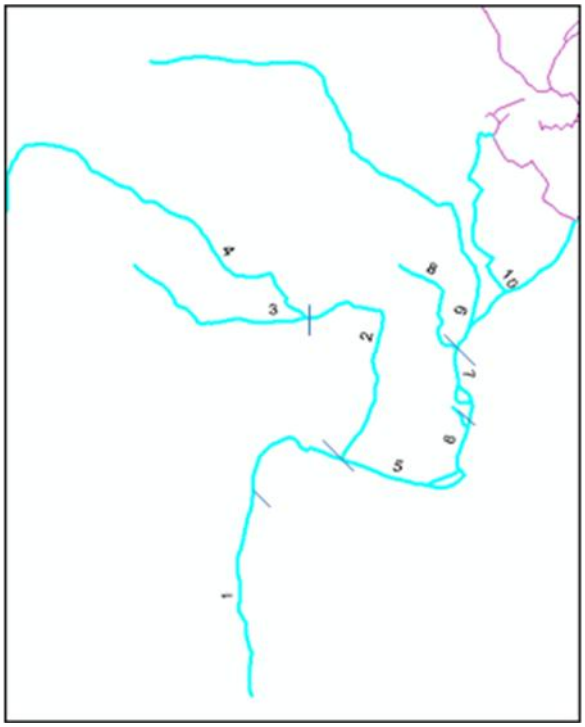

Figure 5.3. Example river network illustrating the component included in the model simulation (blue line) and the reach labels (1-10).

Within the RiverReach tool there are options for calculating the wetted area of the reach, the distance from the downstream end of the reach to the most downstream point of the study river basin, and for generating a matrix which shows how all the reaches are connected. The wetted area and distance values for each reach are

constructed in the map table within the ArcGIS map file, so the user needs to copy and paste these into the **ReachDefinitions.csv** and **DistanceFromSea.csv** files, respectively (Figure 5.4.).

Reach Definitions:					Distance from lower end of reach to bottom of study area				
Length (km)	Width (km)		Reach label (description)		Reach Number	distance (km)			
16.9	0.0177		Reach 1 (starting at tidal limit)		1	0			
9.4	0.0219		Reach 2		2	16.9			
5.2	0.0313		Reach 3		3	26.3			
18.4	0.0260		Reach 4		4	26.3			
3.7	0.0189		Reach 5		5	16.9			
2.3	0.0265		Reach 6		6	20.6			
2.9	0.0077		Reach 7		7	22.9			
4.1	0.0143		Reach 8		8	25.8			
22.6	0.0609		Reach 9		9	25.8			
19.8	0.0302		Reach 10		10	256.3			

Figure 5.4. Example configurations of the ReachDefinition.csv and DistanceFromSea.csv files, derived from the river network illustrated in Figure 5.3.

The RiverReach tool also allows the user to define the location and impact of in-stream structures to the movements of eels. This feature is important in comparing the potential effects of these structures, and benefit of their mitigation or removal. As noted above, reach boundaries should coincide with the locations of significant in-stream structures. The user completes a table within the RiverReach tool (Figure 5.5) to define the locations of in-stream structures in terms of their position between two reaches (for example, from Reach 2 to Reach 3), and the proportion of eels that are 'allowed' to move upstream or downstream past the structure. In the example below, the structure between reaches 2 and 3 allows only (0.7) 70 per cent of eels to move upstream but is no barrier to downstream movements (1), whereas the structure between reaches 6 and 7 only allows 40 per cent of eels to move upstream and 90 per cent of eels to move downstream. The RiverReach tool then applies these proportions instead of 1s and 0s in constructing the **ReachPositioning.csv** file (Figure 5.6).

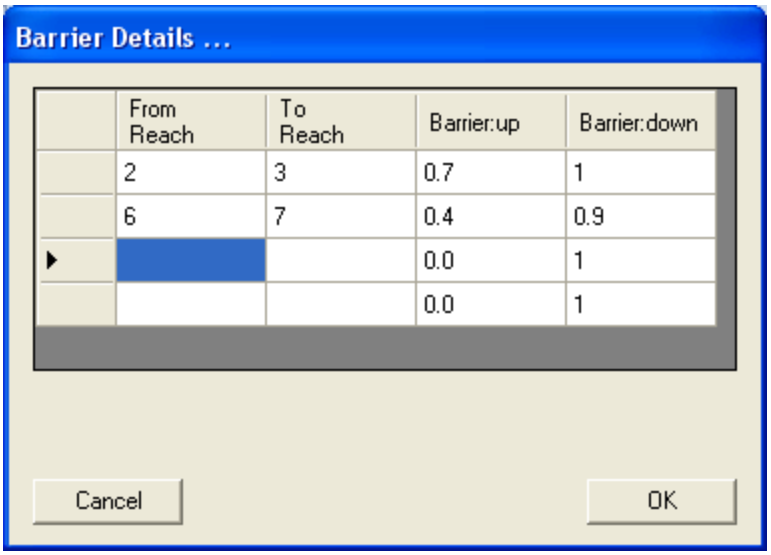

Figure 5.5. Example configuration of the Barrier Details table created in the RiverReach tool where the user can specify the location of each structure and the proportion of potentially moving eels that are able to move upstream or downstream.

Note that these impacts on movement are applied equally to all sizes of eel. In future it may be possible to model different effects for different sizes of eels, but our present understanding of the effects of structures on eel passage is too limited to allow such complexity (see Chapter 6).

The reach connectivity matrix file is created and saved by the tool as the **ReachPositioning.xls** file, but should be converted to a .csv file format so that it can be 'read' by SMEP II. The reaches are shown in the rows and columns, with a '1' in each cell corresponding to the combination of two reaches that are directly connected. In the example below (Figure 5.6), reaches 1 and 2 are connected. Note that the cell on the diagonal for reach 1 should contain a '1' whereas the cells on the diagonal for all other reaches should contain '0's. Those values greater than 0 but less than 1 represent the impact of in-stream structures at the reach boundaries (see above).

Reach number	1	2	3	4	5	6	7	8	9	10
1	1	1	0	0	1	0	0	0	0	0
2	1	0	1	1	1	0	0	0	0	0
3	0	0.7	0	1	0	0	0	0	0	0
4	0	1	1	0	0	0	0	0	0	0
5	1	1	0	0	0	1	0	0	0	0
6	0	0	0	0	1	0	0.9	0	0	0
7	0	0	0	0	0	0.4	0	1	0	0
8	0	0	0	0	0	0	1	0	1	0
9	0	0	0	0	0	0	0	1	0	1
10	0	0	0	0	0	0	0	0	1	0

Figure 5.6. Example configuration of the ReachPositioning.csv file, derived from the river network illustrated in Figure 5.3. The diagonal values are shown in red font, and the barrier proportions are shown in blue font (see below).

In addition to the GIS-based habitat description files, the user can specify trends in habitat or environmental quality for each reach, and for each year of the simulation. The information is provided in the **EnvHabScores.csv** file, an example of which is provided in Figure 5.7. If the habitat quality within a particular reach is considered to impact on the production of eels, this can be represented in the file as value ranging from 0 to 0.99: 1 represents the 'ideal', no impact situation. SMEP II then applies this proportion to the Maximum Biomass Density (*MaxBDensity* in **Parameters.csv**) to find the maximum biomass of eels that the reach can sustain. Note the default is for ideal habitat quality in all reaches, which is selected as option 0 in the **First_File.csv**.

At present, we have a very limited understanding of the influences of habitat on production independent of distance from the sea and density dependent effects. There are several ongoing research programmes to improve on this knowledge and it is anticipated that a more quantitative simulation will become available in the future (see Chapter 6).

Habitat Quality Index										
The EnvHabScore is multiplied by the MaxBDensity (see Parameters.csv) to find the maximum biomass that each reach can sustain										
	Reach:									
	1	2	3	4	5	6	7	8	9	10
Time (y)										
1	1	1	1	0.1	1	1	0.65	1	1	1
2	1	1	1	0.2	1	1	0.65	1	1	1
3	1	1	1	0.3	1	1	0.65	1	1	1
4	1	1	1	0.5	1	1	1	1	1	1
5	1	1	1	0.6	1	1	1	1	1	1
6	1	1	1	0.7	1	1	1	1	1	1
7	1	1	1	0.8	1	1	1	1	1	1
8	1	1	1	0.9	1	1	1	1	1	1
9	1	1	1	1	1	1	1	1	1	1
10	1	1	1	1	1	1	1	1	1	1
11	1	1	1	1	1	1	1	1	1	1
12	1	1	1	1	1	1	1	1	1	1
13	1	1	1	1	1	1	1	1	1	1
14	1	1	1	1	1	1	1	1	1	1
15	1	1	1	1	1	1	1	1	1	1

Figure 5.7. Example configuration of the EnvHabScores.csv file for a river network with 10 reaches, simulating 15 years of eel production. Cell values are the proportion of the Maximum Biomass Density of eels that the reach can sustain (0-1). Reaches 4 and 7 are of less than ideal habitat quality in year 1, but habitat quality is improved and attains the ideal state in years 9 and 4, respectively.

It is anticipated that the user will construct a number of different reach file sets to test scenarios encompassing different productive areas, opening or closing parts of the catchment, improving habitat quality, and so on.

5.1.4 Describing the eel stock from survey data

Where data are available to characterise the eel stock in the study basin, these can be incorporated within the model application: historic data can be used in setting the target, recent data can be used in estimating present escapement, and projections into the future can be used to examine possible effects of management actions.

Eel population data for survey sites are inputted using the **UserInputLFperReach.csv** file, and each survey site is assigned to a reach according to the reach numbering system defined by the user (see above). Each reach is characterised by the proportion (per cent) of females amongst differentiated eels; the total density of eels (numbers per 100m^2); and a length frequency distribution for the surveyed population.

The sex ratio at each site is expressed as the proportion of females amongst the differentiated population. Given that identifying gender requires destructive sampling, it is not anticipated that the sex ratio will be measured for every survey, or indeed in all likelihood for even most surveys. In the absence of such data, therefore, the proportion of females in any survey population can be estimated using the following assumptions (after Bark *et al.,* 2007):

- all eels shorter than the differentiation length (default 200mm) are undifferentiated and therefore excluded from the calculation;
- all eels greater than 450mm in length are females;
- the proportion of females in each class of the intermediate length range (200-450mm) is the same as the whole-river proportion for this length class, or from a similar river (the default value).

In the absence of sufficient data on sex ratio of eels in the study river, the user may apply the relationship developed by Bark *et al.* (2007), based on comparisons of whole-river mean densities and proportions of females:

$$\% \text{ Female} = -73.7 * \log \text{Density (eels per m}^2)^{-8.89}$$

Note that this relationship is developed for density of eel per m^2, and not per $100m^2$ which is the standard unit area used in this report for the application of SMEP II.

This relationship suggests that about 25 per cent of eels will be female in a density of 40 eels per $100m^2$, whereas a density of 10 eels per $100m^2$ will give about 50 per cent female. However, Bark *et al.* acknowledge that their dataset was quite small in terms of numbers of eels sampled (1,400) and rivers (9), and more comprehensive sampling within and between river basins is required in order to establish a robust relationship (see Chapter 6).

The local density of eels will usually be based on a 'depletion' method of estimating numbers of eels, rather than the total catch. It is unlikely, however, that sample sizes will be large enough to allow depletion-based estimates for each length class. Therefore, the length frequency distribution will probably be based on the actual catch of eels. Thus, even though we know that 'catchabilities' often differ between length classes of eel (small eels are usually more difficult to catch), we assume that the length distribution of the catch represents that of the local population.

The number of eels in each length class will be expressed as a proportion of total catch or population estimate. We recommend that the length frequency distribution is constructed using a relatively short length class, for example 10mm. This does result in a relatively large number of length classes (100 for 0-1,000mm distribution) and hence a large table. However, as modelled eels 'grow' by being assigned from one length class to the next per time step, it is important to use a length class shorter than the annual growth increase (default 20mm) in order to avoid unrealistic increases in growth per time step.

When observed eel data are incorporated within the model simulation, SMEP II requires that there are eel data for every reach. If the user does not provide eel data for any reach, the model is run on the basis that the reach contains no eels at the start of the simulation. This would be appropriate for a 'new habitat' scenario, where an area of habitat is currently unavailable to eels but may become available through management actions. However, a starting condition with zero eels would not be appropriate for other situations where the user may choose to include such reaches, for example where no survey data are available, but a fishery or stocking is to be simulated, or where two or more significant tributaries join the river within the reach. In such circumstances, and in the absence of any other information, the user assumes that the nearest surveys in neighbouring reaches are representative of the eels in the no-data reach.

Ideally, the results of each survey would accurately represent the local eel stock throughout that reach. In reality, river basin habitats in England and Wales are diverse and it is highly unlikely that data from sampling some $100\text{-}200m^2$ wetted area will accurately represent the eels over a reach length of several kilometres, especially in riverine environments. Research is ongoing on the influence of habitat on eel production. At present, however, in the absence of more information, the user must assume that the eels between two survey sites follow a stepwise change in character with the step(s) located at one or more arbitrary points between the sites. The issue then is whether there is one step or many. The simplest option is to assume a single

step change midway between the two sampling sites and that this will define the boundary between the two reaches.

A more complex option is to assume that the change in characteristics is gradual between the two sampling locations - this change can then be represented by a series of smaller reaches. The form of the change could be linear, but there is a body of evidence in the literature to suggest an exponential decline in density of eels with increasing distance from the sea (Knights *et al.*, 2001; Ibbotson *et al.*, 2002), and that this relationship is moderated by gradient (Aprahamian *et al.*, 2007) such that:

$$y = ae^{-bx}$$

where *y* is the density of eels (per $100m^2$), *x* is the distance upstream from the tidal influence (km), *a* is the density of eels at the tidal influence (that is, where $x = 0$), and *b* is the instantaneous rate of decline (per km); and:

$$b = ce^{hg}$$

where *c* is the hypothetical instantaneous rate of density decline with no gradient (that is, $g = 0$), *g* is the mean river gradient from source to tidal influence, and *h* is a constant.

The analysis of eel density data for 12 river basins in England and Wales yielded values of $c = 0.0284$ (±0.0058) and $h = 96.73$ (±55.44) (Aprahamian *et al.*, 2007). Therefore, the user may elect to apply this relationship in extrapolating between the two sampling points, and in selecting the locations of boundaries between reaches.

Note that it is not appropriate to allow SMEP II to automatically ‘fill in’ the reaches that have no population data, because this would be achieved by distributing the eels in the reaches with data across more reaches, thereby reducing the density of eels in each reach – there is no facility for automatically adding more eels to the ‘empty’ reaches. New eels can only be introduced by recruitment to the river as a whole (as opposed to movement between reaches), which will affect the density of eels in all reaches.

The eel density/distance/gradient relationships reported above have been developed on the basis that there are no obstructions to the upstream dispersal of eels. However, potential obstructions to eel passage exist in many (perhaps most) river basins in England and Wales. The obvious obstructions are in-stream structures like weirs and dams, but large bodies of standing water may act as a ‘sink’ for eels, slowing their upstream dispersal. At present we have little knowledge from which to quantify the obstructive nature of in-stream structures or standing waters and, therefore, it is very difficult to model their potential effects.

It is clear, however, that these obstructions can influence the dispersal of eels and their densities and distribution upstream. For example, densities of eels measured at sites throughout the rivers Blyth and Ellen reveal declining trends in eel density with distance from the sea (Bark, Knights and Williams, unpublished data from Defra project SF0236). However, densities in the Blyth are high at the first two survey sites, up to 8km from the sea, but then relatively low throughout the remainder of the river network (Figure 5.8). Similarly, the Ellen data suggest three zones approximately defined as 0-4km, 5-20km and 20km+ (Figure 5.9).

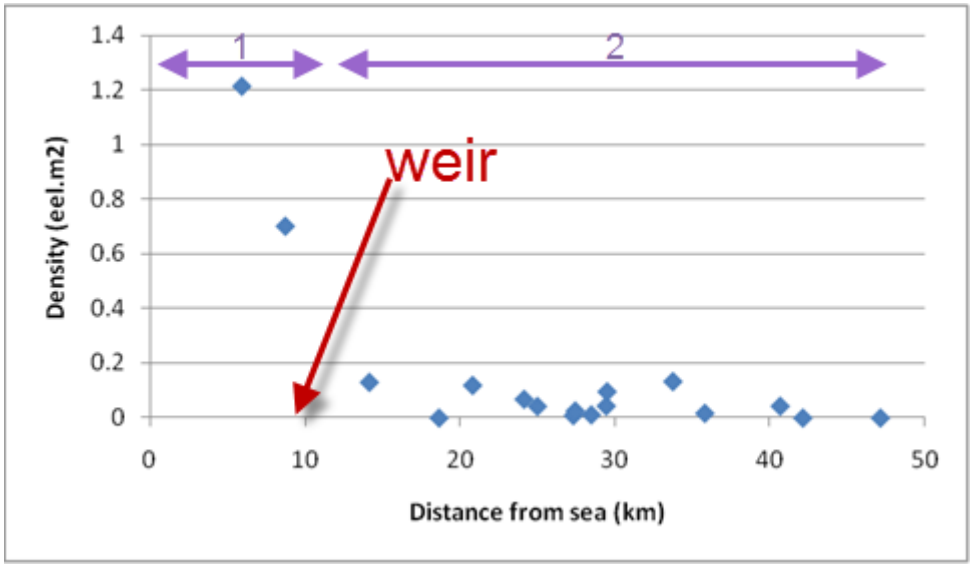

Figure 5.8. Densities of eel at survey sites along the length of the River Blyth, Northumberland, sampled by eel-specific electrofishing by Bark, Knights and Williams (unpublished Defra data). The red arrow indicates the location of a substantial weir that appears to affect the distribution of eels. The purple lines and numbers indicate the two putative zones of different eel density.

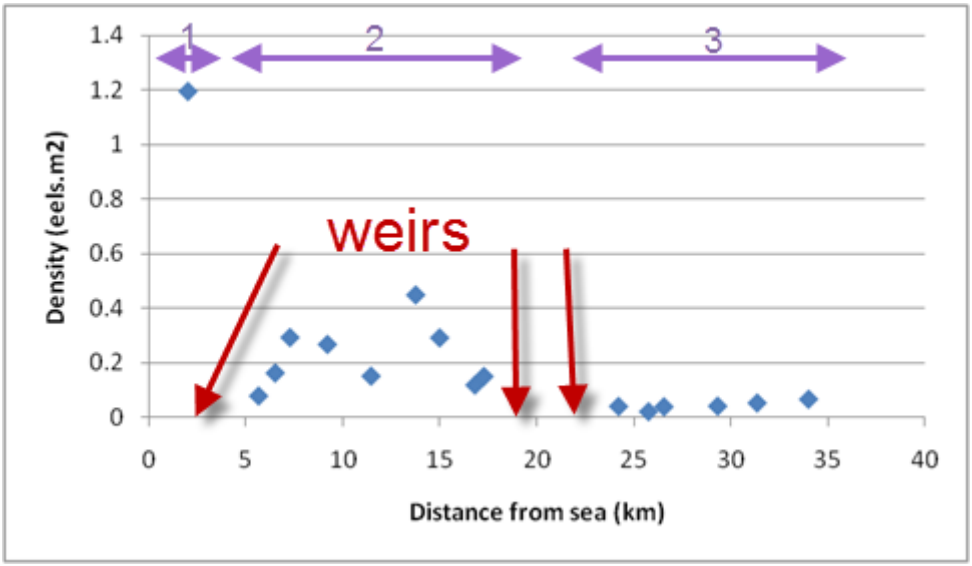

Figure 5.9. Densities of eel at survey sites along the length of the River Ellen, Northumberland, sampled by eel-specific electrofishing by Bark, Knights and Williams (unpublished Defra data). The red arrows indicate the location of substantial weirs that appear to affect the distribution of eels. The purple lines and numbers indicate the putative eel density zones.

The boundary at 8km on the Blyth corresponds with the location of an obstruction ('Stepping Stones' weir) which has a drop of about 4m according to LIDAR data (J. Gregory, Environment Agency, pers. comm.). On the Ellen, there are three weirs between the first and second zones, with drops ranging from 0.3 to 0.5m, and two structures around the boundary between the second and third zones, with drops of 0.7 and 1.3m. Thus, the location and characteristics of in-stream structures may influence

the patterns of eel density in addition to distance from the sea. The results suggest that sampling should be stratified according to locations upstream and downstream of structures which are deemed to pose a significant obstruction to the movement of eels.

Clearly there are several large gaps in our knowledge in the process of dispersal of eels, and these limit our ability to advise on the most appropriate method of extrapolating data between two survey sites, and on the most appropriate number and distribution of survey sites throughout a river basin. Suffice it to say that prior knowledge from earlier surveys is very valuable in deciding where best to locate sampling sites.

SMEP II does not 'recognise' any differences between rivers and lakes – a lake is incorporated as a relatively wide reach with a particular habitat quality potential. Where the user considers that a lake acts as a 'sink' and therefore delays the upstream dispersal of eels, this can be simulated by introducing a proxy obstruction that reduces the upstream dispersal of modelled eels compared to the dispersal rate that would be expected between one river reach and the next.

5.1.5 Anthropogenic impacts and inputs

SMEP II can simulate the 'impact' of anthropogenic factors such as fishing and turbines, and the effects of stocking. The options for fishing and stocking are activated in the **First_File.csv**. As the mortality associated with turbines is in effect a removal of eels from the production, in other words, a 'catch', there is no specific data input for turbines and their impact is simulated either as a mortality rate (per cent) associated with downstream passage past a barrier at a reach boundary (see Figures 5.5 and 5.6) or as a fishery.

Fishing

Fishing can be described in SMEP II in two ways and in two input files, depending on the available data: numbers caught by length class per gear type (**TotalCatchByLength.csv**); or numbers caught by stage (undifferentiated, yellow or silver) per gear type (**TotalCatchByStage.csv**). All fishing data are related to reaches, seasons and years. Therefore, it is possible for the user to vary both the location and impact of fisheries, and simulate changes in the control of fisheries.

The format of the **TotalCatchByLength** and **TotalCatchByStage** files is the same, requiring information for the year, season, reach, and gear that correspond to each catch event, and the number of eels caught. The only difference is that the catch is described as either numbers per length class or numbers per stage. Only one of the two files is needed in each model run and which file is determined by the value that the user chooses for option 'fishing' in the **Parameters.csv** file.

There is no upper limit to the number of fishing events that the user can include in these files. Given that the model uses length classes, each length provided in the **TotalCatchByLength** file is automatically translated into a length class. So, if the model uses length classes of 10mm length and the user describes catches for eels of length of 235mm, the model will assume that those catches are taken from the eels that are in the class that covers lengths from 230mm to 240mm. For this reason, there is no need to include two different events in the **TotalCatchByLength** file to describe catches in a given reach and time step that are assigned lengths that fall within the same length class.

Licensed fishers are required by the Environment Agency to report the number of days fished per month, the location and type of water (river, still, estuary/coastal), and the total weight of eels or elvers caught and retained. Given these reporting requirements, it is likely that expressing catch as numbers caught per stage will be the most common method to describe fishery impacts in the application of SMEP II. However, this requires an assumption about the length structure of the catch (see below), and it would be better if length data were available for the catch and the user completed the **TotalCatchByLength.csv** file.

In the absence of fishery controls, the model assigns the catch of undifferentiated eels to a uniform length distribution with boundaries based on the minimum length of recruits (*MinRecLength*) and the length at differentiation (*DiffLength*), which are defined in the **Parameters.csv** file. Similarly, the yellow eel catch is assigned lengths between *DiffLength* and the mean length of female silver eels (*MatInflectionF*). As there are two functions describing the probability of eels becoming silver at various lengths, these probabilities are used to assign a length distribution to the silver eel catch file.

For the eel fisheries of England and Wales, however, the glass eel fishery catches eels of a small length range, and there is a minimum allowed landing size of 300mm for the yellow and silver eel fishery. Therefore, the undifferentiated catch (as a mortality) can only be the glass eel and, as such, is assigned lengths according to the length distribution of recruits defined in the **Parameters.csv** file (mean length and SD, minimum and maximum limits). Likewise, the minimum length of the yellow eel and silver eel catches is set at 300mm. Figure 5.10 provides an example configuration of the **TotalCatchByStage.csv** file, with a glass eel fishery that catches 300,000 eels (100kg) in Reach 1 every spring, a yellow eel fishery that catches 1,000 eels in Reach 4 every spring, and a silver eel fishery that catches 500 silver eels in Reach 1 in the autumn of years 1 and 2, after which it is closed.

Total_Catch:					
Number_of_gears:	3				
Year_of_run:	Season:	Reach:	Stage:(U,Y,S)	Gear_Number:	Total_catch_N:
1	2	1	U	1	300000
1	2	4	Y	2	1000
1	3	1	S	3	500
2	2	1	U	1	300000
2	2	4	Y	2	1000
2	3	1	S	3	500
3	2	1	U	1	300000
3	2	4	Y	2	1000
3	3	1	S	3	0
4	2	1	U	1	300000
4	2	4	Y	2	1000
4	3	1	S	3	0
5	2	1	U	1	300000
5	2	4	Y	2	1000
5	3	1	S	3	0
6	2	1	U	1	300000
6	2	4	Y	2	1000
6	3	1	S	3	0

Figure 5.10. Example configuration of the TotalCatchByStage.csv file for a river network, simulating six years of fishing exploitation. Glass eel and yellow eel fishing occurs throughout the period but the silver eel fishing ceases after year 2.

Turbines

As noted above, turbines are modelled either as a barrier-induced mortality rate (per cent) or as a proxy fishery. Since the associated dam or weir is likely to form the boundary between two reaches, the user can choose to apply the turbine mortality to the upstream or downstream reach. Although yellow eels may be entrained in turbines, we assume that turbine-induced mortality is mostly an impact on downstream migrating silver eels. Therefore, we recommend that the turbine mortality or 'fishery' is assigned to the reach immediately upstream of the dam or weir.

In the absence of data on the mortality caused by turbines within a specific installation, we anticipate that the user will apply mortality rates published in the scientific literature (see Chapter 4). In the absence of *a priori* knowledge on the number of eels encountering the turbines, therefore, it is most appropriate to describe the mortality rate using the **FishingPractices.csv** file, as this provides more flexibility in describing the mortality than simply applying a barrier-associated rate. Here, the user describes the year and season when the mortality occurs, the reach location, the parameters to define the length-based mortality curve (L50, L75, D50, D75), the number of days during which the mortality occurs (set to 91 for a full season), and the catchability coefficient (mortality rate). Longer eels are more likely to be damaged in passage through turbines (Larinier and Travade, 2002), though variations in turbine design and operation, and indirect impacts from pressure changes and rapid changes in flow velocity, mean it is unlikely that there is an absolute minimum length below which eels are not impacted.

The L50 and L75 values are those lengths above which 50 and 75 per cent of eels are impacted by the turbine. Setting similar values for these two parameters effectively specifies the length below which very few eels will be impacted, in other words a *quasi*-minimum length. The D50 and D75 values define an upper limit of the mortality curve, but if turbines are assumed to impact all eels above a minimum length, these values should be set to zero. The example in Figure 5.11 shows the data configuration for a turbine mortality on the autumnal silver eel migration in Reach 3, which impacts on eels above 300mm in length, occurs throughout the season and with a mortality rate of 20 per cent. The mortality occurs in years one to five, but the impact is removed from year six onwards.

Fishing_data:								
Year_of_run:	Season:	Reach:	L50:	L75:	D50:	D75:	Effort:	Catchability:
1	3	3	300	300	0	0	91	0.2
2	3	3	300	300	0	0	91	0.2
3	3	3	300	300	0	0	91	0.2
4	3	3	300	300	0	0	91	0.2
5	3	3	300	300	0	0	91	0.2
6	3	3	300	300	0	0	91	0
7	3	3	300	300	0	0	91	0
8	3	3	300	300	0	0	91	0
9	3	3	300	300	0	0	91	0
10	3	3	300	300	0	0	91	0

Figure 5.11. Example of the FishingPractices.csv file configured to represent the mortality associated with a turbine facility located at the lower end of Reach 3. The turbine causes a mortality of 20 per cent on eels above 300mm length in the third season (autumn), but this is reduced to zero after year five.

Stocking

If the user wishes to simulate the benefits of stocking eels, then the stocking events are described in the **Stocking.csv** file. The user defines the year and season when stocking takes place, the reach that is stocked, and the mean length and number of eels stocked. Figure 5.12 illustrates a Stocking.csv file where glass eel with mean length 80mm are stocked into Reach 6 in years five, six and seven, with 120,000 being stocked in the first year and then 60,000 each year thereafter.

Restocking:				
Year:	Season:	Reach:	Length (mm):	Number:
5	2	6	80	120000
6	2	6	80	60000
7	2	6	80	60000

Figure 5.12. Example of the Stocking.csv file configured to represent the spring-time stocking of 120,000 glass eel (mean length 80mm) into Reach 6 in year five, with further stockings of 60,000 each in years six and seven.

5.2 Model outputs

SMEP II reports the results of simulations in a series of .csv files that provide, for each reach in every year: the density and biomass of undifferentiated, male and female yellow eels; numbers and weight of emigrating male and female silver eels; the proportion of females; and the numbers and weight of ‘catch’.

End-of-run files provide summaries of density and biomass of undifferentiated, male and female yellow eels, biomass of male and female silver eels, and ‘catch’ (numbers and biomass) of undifferentiated, yellow and silver eels, and the length frequency of eels, stages and sexes in each reach.

These output files are described below in relation to the illustrations of example model applications.

5.3 Example applications

We have simulated a relatively small river basin to illustrate how SMEP II can be used to set the management target (that is, 40 per cent of the silver eel biomass expected in the absence of anthropogenic impacts); estimate present escapement of silver eels (compliance with the target) and future escapement with and without management interventions; establish intermediate or proxy targets to monitor in the absence of silver eel data; and use the future predictions to inform cost-benefit analysis of management options. The geography of the river basin and the yellow eel survey data are based on those for a real river basin, but impacts are simulated to illustrate the application of SMEP II in various scenarios. Therefore, the river basin is not named here.

A branching topology riverline was extracted from the Environment Agency-CEH riverline GIS dataset and the River Reach tool was used to construct a reach file based on 15 reaches (Figure 5.13), with lengths, widths and distances to the most downstream location of the basin as shown in Figure 5.14, and a total wetted area of about 221.4 hectares.

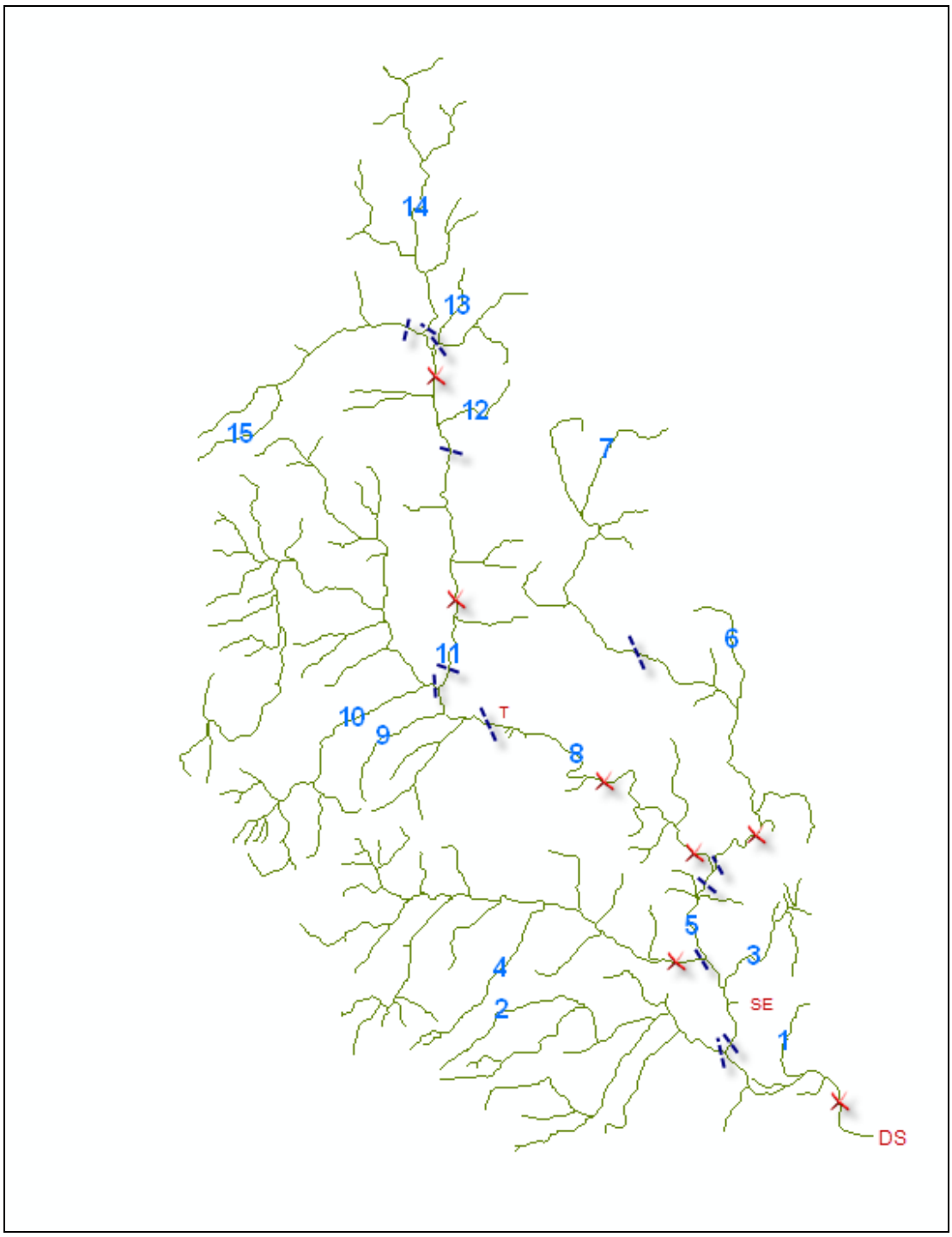

Figure 5.13. Schematic representation of the river network GIS map used in the example applications of SMEP II. The riverline is shown in green, the boundaries between the 15 reaches are shown as blue dashed lines, the most downstream location is shown as DS, the survey sites are shown as red crosses, the silver eel fishery in Reach 3 is shown as SE, and the turbine between Reaches 8 and 9 is shown as T.

Reach label (description)	Length (km)	Width (km)	distance downstream (km)
Reach 1	6.412	0.02	0
Reach 2	10.944	0.02	6
Reach 3	3.075	0.03	6.4
Reach 4	13.275	0.03	7.9
Reach 5	2.796	0.02	9.5
Reach 6	5.155	0.03	10
Reach 7	14.969	0.01	15
Reach 8	10.894	0.01	12.2
Reach 9	1.365	0.06	23.2
Reach 10	15.514	0.03	24.5
reach 11	7.275	0.01	24.7
Reach 12	3.294	0.02	31.8
Reach 13	3.449	0.01	34.1
Reach 14	8.58	0.01	34.6
Reach 15	10.17	0.01	34.8

Figure 5.14. Extracts from the ReachDefinitions.csv and DistanceFromSea.csv input files used in the example applications of SMEP II for the river basin shown in Figure 5.13.

Data on the density (numbers and biomass), length structure and sex ratio of yellow eel are simulated for seven sites (Figure 5.13), with data chosen with reference to results from typical Environment Agency eel-specific electrofishing surveys. No direct measures of recruitment are available.

5.3.1 Establishing the long-term management target

Assuming there are no historic data for the yellow eel population in the river basin, as is the case for most river basins in England and Wales, the approach for estimating the 'pristine' potential escapement of silver eel, and hence the 40 per cent target, is to start with a river basin empty of eels, and then apply appropriate levels of recruitment over an extended time series until the annual silver eel production reaches an equilibrium. Note that, in the absence of anthropogenic impacts on the eels, silver eel escapement equals silver eel production. We define escapement as the amount of eel that emigrate from the lower boundary of the study basin (DS).

Using this approach, we start with the 'empty' river basin and reach definitions as shown in Figure 5.14, assume a pristine environment and a population at equilibrium after an arbitrary chosen long period of 200 years (Figure 5.15), and default life history parameters obtained from Chapter 4 (Figure 5.16). In the absence of quantitative information on glass eel / elver recruitment to rivers in England and Wales, simulations are run with annual recruitment varying from 500,000 to 5 million individuals.

Set_the_main_assumptions_for_the_model	Choices
Is_it_Deterministic_(D)_or_Stochastic_(S)?	D
Will_it_use_observed_data?_(Y_or_N)_(only_in_detrministic_mode)	N
FOR STOCHASTIC SIMULATIONS	
Do_you_want_Fixed_(F)_or_Random_(R)_seed?	F
How_many_simulations_are_required?	1
SET MAIN MODEL STRUCTURE	
What_is_the_maximum_length_of_eels_(mm)	1000
What_length_class_(mm)_is_used?	10
How_many_reaches_in_the_river_network?	15
Number_of_years_to_project_the_population_forward	80
INITIALISATION OF POPULATION	
Does_the_population_start_in_theoretical_equilibrium_or_known_st	1
The_equilibrium_simulation_will_run_for_how_many_years?	200
EXTERNAL FACTORS	
What_is_the_recruitment_pattern?	0
Will_fishing_be_represented?	0
What_environmental_conditions_will_apply?	0
Will_stocking_be_included?	0

Figure 5.15. Extract from the First_File.csv input file used in the example applications of SMEP II for the river basin shown in Figure 5.13.

Eel life history process parameters:	Value:		Eel life history process parameters:	Value:
default_timestep	0.25		NATURAL MORTALITY:	
			InputMortality	0
GROWTH:			NMgamma	0.15
choice_of_model	1		NMgammaMax	0.3
GrowthSeason	3		NMgammaMin	0.15
GrowthTimeStep	1		RestockingMortality	0.2
LINEAR MODEL - FEMALES				
growth_slopeF	2.00E+01		SILVERING:	
			MatCurveF	0.0258
LINEAR MODEL - MALES			MatInflectionF	550
growth_slopeM	20		MatCurveM	0.0640
			MatInflectionM	350
LINEAR MODEL - UNDIFFERENTIATED				
growth_slopeU	20		LENGTH-WEIGHT:	
CARRYING CAPACITY / ENV QUALITY:			LWalpha	5.42E-07
MaxBDensity	2600		LWbeta	3.196
RECRUITMENT:			MOVEMENT:	
MeanRecruits (millions)	0.5 to 5		RelativeTransition	2
CVMeanRecruits	0.005		MaxUndiffMovementRate	46
MeanLength	70		MaxYellowMovementRate	10
SDLength	20		MaxSilverMovementRate	120
MinRecLength	50			
MaxRecLength	100			
SEXUAL DIFFERENTIATION:				
DiffLength	200			
UndiffSatLevel	0.95			
lengthAllFemale	450			
OgiveType	1			
SDinflection	0.5			
Diff_range	0.45			
Sdpower	1.2			
SDslope	1			

Figure 5.16. Extract from the Parameters.csv input file used in the example applications of SMEP II for the river basin shown in Figure 5.13.

Results

SMEP II provides 14 output files that detail stage- and sex-specific densities and biomasses, and length frequencies of yellow eel per reach per year, numbers and biomass of silver eel produced per year, and stage-specific catch as numbers and biomass. However, as the management target is described as a biomass of silver eels, for this example we limit discussion of the results to those of silver eel numbers, biomass and the ratio of females to males.

Varying annual recruitment from 500,000 to 5 million elvers results generally in increasing silver eel biomass, rising from 674 to 6,024kg (Figure 5.17). Despite an initial 200 years to equilibrate the local population, however, annual silver eel biomass becomes increasingly unstable at recruitments greater than 3 million. For example, silver eel biomass at recruitment of 5 million varies by more than 1,000kg between years despite the population apparently being at 'equilibrium'. This instability at higher levels of recruitment arises because the standing biomass of lower reaches that receive recruits is already at the designated maximum area-specific biomass (**Parameters.csv**: *MaxBDensity*). Repeated high recruitment under such conditions results in exceptionally high levels of natural density-dependent mortality amongst the recruits and other eels in these reaches. This, in turn, allows high recruitment the following year to fill 'capacity' and repeat the process, thus ultimately producing the cyclical instability in silver eel production. This is illustrated to some extent by the irregular increase in silver eel biomass from 3 to 4.5 million in Figure 5.17.

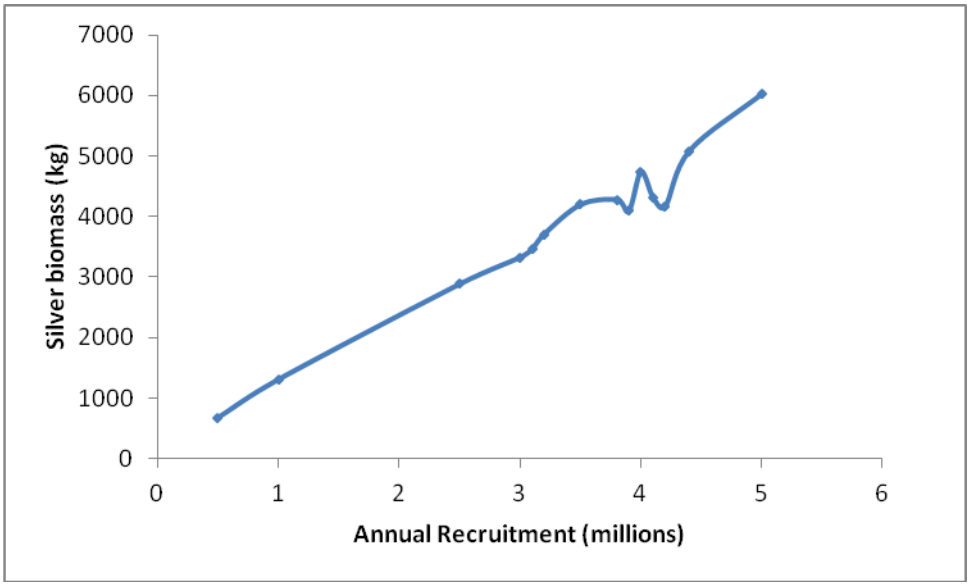

Figure 5.17. Annual production of silver eel (kg: blue line) of the study river basin under equilibrium conditions, with annual recruitment varying from 500,000 to 5 million elvers.

As about 3 million recruits is the maximum that produces a stable silver eel biomass output, we select this as the reference 'pristine' state from which to estimate the management target. SMEP II reports a silver eel output of about 3,325kg per year,

which equates to about 15kg per hectare, averaged across the entire study area. The management target would therefore be 40 per cent of this: 1,330kg or about 6kg per hectare.

Increasing recruitment results in substantial changes in the number of male silver eels estimated to be produced, rising from about 3,300 for 500,000 recruits to 32,000 for 3 million recruits (Figure 5.18). In contrast, the number of female silver eels is far smaller, and a 10-fold increase in recruitment results in an increase from about 1,600 to 2,900 females. Not surprisingly, therefore, the sex ratio of the silver eel output alters with increasing recruitment, with the percentage of females declining from about 32 per cent at 500,000 recruits to about 7 per cent at 3 million recruits (Figure 5.18).

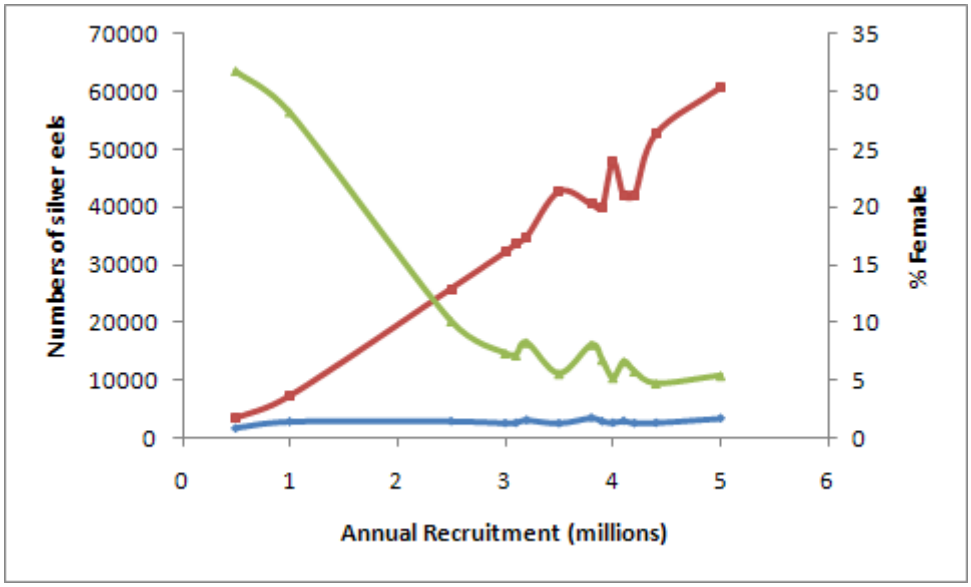

Figure 5.18. Numbers of male (red line) and female (blue) silver eels produced from varying levels of recruitment, and the resultant % females amongst the emigrants (green). Note that silver eel production is unstable at recruitment above about 3 million, but the data are shown here for comparison with Figure 5.17.

Eel population dynamics in attaining equilibrium

As described above, the normal 'setting the target' procedure would be to examine the silver eel production from an eel stock in equilibrium (**First_File.csv**: *Initialisation of Population*; option 1). It is interesting in terms of the modelling of eel population dynamics, however, to examine the development of the population towards equilibrium when starting from a basin with no eels, that is, prior to achieving equilibrium. To achieve this, we selected option 2 in the **First_File.csv**: '*What is the starting condition*', allowing the starting eel population to be described in the **UserInputLFperReach.csv** file, but configuring that file so that there were no eels (that is, 0 in each cell). We applied the 3 million recruits annually and ran the simulation for 80 years.

The size of the population at the beginning of this calculation is equal to the 3 million elvers that are recruited to the system in the first year of the calculations. Figure 5.19 displays the trends in average densities and biomasses of eels across the river basin. Densities peak at 212 eels per 100m^2 after 18 years, then decline a little before stabilising at 210 eels from year 32 onwards. Biomass peaks at 1,906g per 100m^2 in

year 23, a little later than density, but also then declines slightly to stabilise at about 1,780g in year 33.

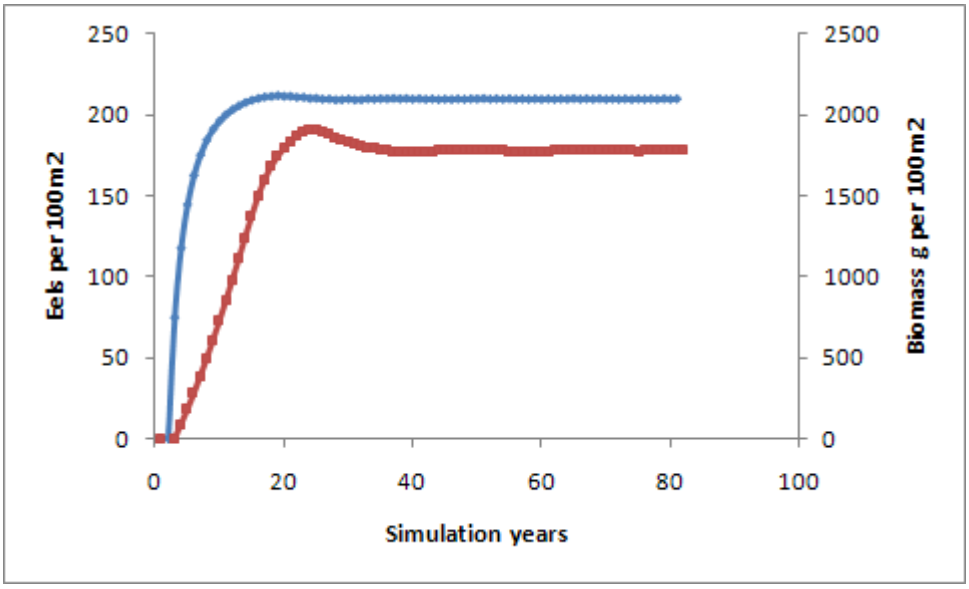

Figure 5.19. The development of the yellow eel population towards equilibrium, at recruitment of 3 million elvers per annum. The average whole-river density per 100m^2 is shown by the blue line, and the average whole-river biomass per 100m^2 is shown by the red line.

Silver eel production begins in year 6, then rapidly rises in both numbers and total biomass to peak at levels of about 36,400 and 3,775kg in years 24 and 25, respectively. Annual production varies from year to year thereafter, but the variations are small (Figure 5.20) and the population can be considered at equilibrium.

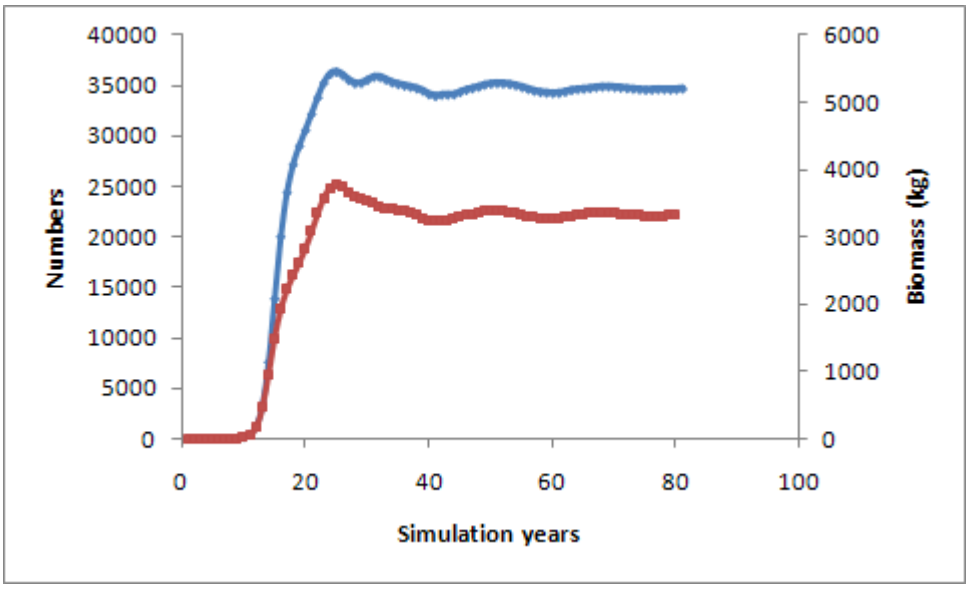

Figure 5.20. The annual silver eel production in numbers (blue line) and biomass (kg: red line) from the yellow eel population as it develops towards equilibrium, at recruitment of 3 million elvers per annum.

The sex ratio of the initial, recruiting population is 50:50 as this is the default assumption for undifferentiated glass eels, that is, they have an equal probability of becoming male or female. However, yellow eel densities in the river reaches increase rapidly at this high level of recruitment, and males dominate the silver eels from their first year of production, reaching an equilibrium level of 80 per cent in year 24.

The study river basin is relatively short, with the upper reaches being ~35km from the sea. The maximum upstream dispersal rate of elvers is 46km per annum, and that of yellow eels 10km per annum (set in the **Parameters.csv** file). In these conditions, SMEP II predicts that elvers would occupy reaches up to 12km from the sea in the first year, but yellow eels would not first occupy the uppermost reaches until years 8-10 of the simulation (Figure 5.21). Given that the maximum upstream dispersal rate of undifferentiated eels is greater than the distance from sea to source, the model understandably predicts that undifferentiated eels will eventually occupy all upper reaches, but only at very small densities, and the majority of eel in these areas would be differentiated yellow eels.

Reach Number	Distance from sea (km)	First year of occupation
1	0	1
2	6	1
3	6.4	1
4	7.9	1
5	9.5	1
6	10	1
7	15	2
8	12.2	1
9	23.2	2
10	24.5	5
11	24.7	4
12	31.8	6
13	34.1	8
14	34.6	9
15	34.8	10

Figure 5.21. Dispersal of yellow eels throughout the 15 reaches of the river basin, represented by the first year when eel densities achieve at least 1 eel per 100m^2 in each reach.

5.3.2 Estimating present escapement

In the absence of any information on the present-day yellow eel stock within a river basin, it is conceivable that the escapement of silver eels could be estimated by projecting forwards in time from the equilibrium state, as derived in section 5.3.1, and applying an appropriate trend in recruitment. Two example recruitment trends are provided in the "**Pre-defined**" data input folder representing:

- the declining trend in average European recruitment (ICES, 2010) in file **EuropeanRec.csv**;
- the declining trend in glass eel recruitment to England and Wales since 1980, based on fishery CPUE (kg glass eels per licence) indexed to the average CPUE from 1980 to 1982, the only data prior to the collapse of catches in 1983 (Walker *et al.,* 2010) in **UKReccruitment.csv**.

However, there is considerable uncertainty associated with each of these trends in terms of their representation of recruitment to any particular UK river basin. The European average recruitment is based on 24 datasets spanning the Mediterranean to Baltic. The UK trend in CPUE is based on glass eel catch reported to the Environment Agency and its predecessors, but it is believed that under-reporting has been considerable and variable between years, and licence sales are a simplistic representation of fishing effort. Therefore, we only recommend this approach to estimating escapement when no other option is available.

A more appropriate method to estimate escapement is to model survey data to characterise the existing eel population. In essence, the model starts with a basin occupied by yellow eels of various sizes and ages, and 'grows and matures' these eels over time to become silver eels. Eel population data for survey sites are inputted using the **UserInputLFperReach.csv** input file. Here we have used typical electrofishing survey data for six reaches in the study basin, and then extrapolated these to the neighbouring reaches where no survey data were available (Figure 5.22) – see *Describing the eel stock from survey data*, above. The other life history processes are described in the same manner as for setting the target – see Figure 5.16.

	Reach 1	Reach 2	3	4	5	6	7	8	9	10	11	12	13	14	15
Prop'n F	0.51	0.53	0.52	0.55	0.53	0.55	0.57	0.57	0.63	0.73	0.68	0.75	0.80	0.82	0.83
Density n.100m2	253.9	188.8	228.3	69.4	173.9	70.4	35.5	57.9	35.3	6.5	11.8	6.0	2.1	1.9	1.6
LF class 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LF class 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0.0698	0.0698	0.0698	0.0303	0.0698	0.0482	0.0482	0.0540	0.0540	0.0022	0.0022	0.0000	0.0000	0.0000	0.0000
9	0.0940	0.0940	0.0940	0.0409	0.0940	0.0650	0.0650	0.0727	0.0727	0.0029	0.0029	0.0000	0.0000	0.0000	0.0000
10	0.1327	0.1327	0.1327	0.0694	0.1327	0.0977	0.0977	0.1063	0.1063	0.0184	0.0184	0.0055	0.0055	0.0055	0.0055
11	0.1294	0.1294	0.1294	0.0732	0.1294	0.0981	0.0981	0.1054	0.1054	0.0246	0.0246	0.0080	0.0080	0.0080	0.0080
12	0.1238	0.1238	0.1238	0.0842	0.1238	0.1012	0.1012	0.1043	0.1043	0.0448	0.0448	0.0219	0.0219	0.0219	0.0219
13	0.0752	0.0752	0.0752	0.0662	0.0752	0.0693	0.0693	0.0671	0.0671	0.0492	0.0492	0.0274	0.0274	0.0274	0.0274
14	0.0740	0.0740	0.0740	0.0723	0.0740	0.0725	0.0725	0.0672	0.0672	0.0631	0.0631	0.0445	0.0445	0.0445	0.0445
15	0.0455	0.0455	0.0455	0.0525	0.0455	0.0493	0.0493	0.0425	0.0425	0.0550	0.0550	0.0463	0.0463	0.0463	0.0463
16	0.0461	0.0461	0.0461	0.0573	0.0461	0.0530	0.0530	0.0442	0.0442	0.0641	0.0641	0.0618	0.0618	0.0618	0.0618
17	0.0292	0.0292	0.0292	0.0407	0.0292	0.0369	0.0369	0.0291	0.0291	0.0499	0.0499	0.0557	0.0557	0.0557	0.0557
18	0.0303	0.0303	0.0303	0.0447	0.0303	0.0404	0.0404	0.0311	0.0311	0.0567	0.0567	0.0692	0.0692	0.0692	0.0692
19	0.0196	0.0196	0.0196	0.0316	0.0196	0.0285	0.0285	0.0211	0.0211	0.0423	0.0423	0.0577	0.0577	0.0577	0.0577
20	0.0208	0.0208	0.0208	0.0349	0.0208	0.0317	0.0317	0.0231	0.0231	0.0480	0.0480	0.0697	0.0697	0.0697	0.0697
21	0.0138	0.0138	0.0138	0.0260	0.0138	0.0227	0.0227	0.0181	0.0181	0.0395	0.0395	0.0496	0.0496	0.0496	0.0496
22	0.0149	0.0149	0.0149	0.0289	0.0149	0.0255	0.0255	0.0200	0.0200	0.0451	0.0451	0.0596	0.0596	0.0596	0.0596
23	0.0099	0.0099	0.0099	0.0229	0.0099	0.0175	0.0175	0.0176	0.0176	0.0368	0.0368	0.0355	0.0355	0.0355	0.0355
24	0.0108	0.0108	0.0108	0.0257	0.0108	0.0198	0.0198	0.0198	0.0198	0.0424	0.0424	0.0427	0.0427	0.0427	0.0427
25	0.0071	0.0071	0.0071	0.0191	0.0071	0.0133	0.0133	0.0151	0.0151	0.0300	0.0300	0.0285	0.0285	0.0285	0.0285
26	0.0078	0.0078	0.0078	0.0217	0.0078	0.0151	0.0151	0.0171	0.0171	0.0348	0.0348	0.0343	0.0343	0.0343	0.0343
27	0.0053	0.0053	0.0053	0.0158	0.0053	0.0102	0.0102	0.0125	0.0125	0.0242	0.0242	0.0237	0.0237	0.0237	0.0237
28	0.0059	0.0059	0.0059	0.0180	0.0059	0.0117	0.0117	0.0143	0.0143	0.0282	0.0282	0.0285	0.0285	0.0285	0.0285
29	0.0040	0.0040	0.0040	0.0131	0.0040	0.0080	0.0080	0.0103	0.0103	0.0197	0.0197	0.0200	0.0200	0.0200	0.0200

Figure 5.22. Extract from the UserInputLFperReach.csv file used to illustrate model application to estimate present silver eel production, and project future production under various management scenarios. Note the extract is truncated at 29 length classes for brevity but the file has 100 length classes (0-1000mm in 10mm length bins).

In the absence of a quantified trend of eel recruitment to the river, the model is projected forwards from a known yellow eel population. Present production can be estimated from a projection run with no recruitment, on the basis that the silver eels produced in the first year represent the production under present conditions and with recruitment at level '*X*'. In the absence of recruitment, however, silver eel production in later years not only declines as eels leave the system, but also changes in character as declining yellow eel densities reduce the density-dependent effects on sex

differentiation, natural mortality and upstream dispersal. As a consequence, the results of projections without recruitment should be ignored beyond the first few years.

The yellow eel population from surveys reflects any impacts from anthropogenic factors already suffered by the undifferentiated and yellow eels. Therefore, such impacts are not included again in this model application. However, the model must be parameterised to include any silver eel mortalities due to anthropogenic impacts, in order to estimate the present silver eel escapement. Here, we simulated a silver eel fishery in Reach 3 taking an annual catch of 100kg (500 eels), and a turbine between Reaches 1 and 2 (Figure 5.13). The silver eel fishery catch is described in the **TotalCatchByStage.csv** file (Figure 5.10), and the turbine mortality is described in the **FishingPractices.csv** file (Figure 5.11).

SMEP II predicts that average annual silver eel production from this standing stock of yellow eels will be about 5,766 male and 2,429 female silver eels. The predicted biomass is 1,079kg, which is 31 per cent of the pristine. Therefore, the river basin escapement of silver eels is below the 40 per cent management target.

5.3.2 Selecting appropriate management measures

The procedures described above allow the user to estimate present silver eel escapement, and to assess this in relation to the management target. The manager may then be required to introduce measures to recover escapement above the target, or to protect the present level of escapement. SMEP II can be used to predict the benefits of reducing or removing anthropogenic impacts.

The first thing to establish is how the escapement might be expected to change over the coming years in the absence of intervention (that is, management measures). This is the baseline position against which to compare the effects of any management measures. However, as noted above, a time series of annual recruitment is required in order to project the stock forwards without affecting silver eel production and characteristics solely because of reducing densities of yellow eel. In the absence of a quantified recruitment trend for the study basin, we can use SMEP II to find the amount of recruitment that ought to produce the ‘observed’ yellow eel stock, as determined by the yellow eel surveys.

Selecting appropriate level of recruitment

The simplest method of identifying an appropriate recruitment level is to assume that the observed stock is at equilibrium, and therefore to repeat the procedure to ‘**Establish the long-term target**’, above, varying the recruitment to find a level that results in a simulated yellow eel stock and silver eel production similar in character to that of the observed stock.

Using this iterative (trial and error) procedure, we find that SMEP II predicts that an annual recruitment of 900,000 glass eels provides a silver eel output similar to that predicted for the observed stock.

This method relies on the assumption that the present stock of eel is at equilibrium. This assumption may be simplistic, however, given the substantial declines in recruitment to European waters over the last three decades. An alternative approach would be to start from the equilibrium state described in the output from the ‘**Establishing the long-term target**’ procedure, and apply recruitment trends based on the assumption that these trends have impacted yellow and silver eel production over a

period of about 30 years, along with all anthropogenic impacts. As with the simplistic approach, however, this approach requires assumptions that the stock was in equilibrium 30 years ago, and that the European or UK reference datasets provide a good representation of changes in recruitment to the study river basin. We recommend that this more complex approach is investigated. However, as the general modelling procedure is the same as that for the 'recruitment-equilibrium' scenario, above, we do not provide further illustrations of this more complex procedure here.

Trends in recruitment

After having identified a suitable starting recruitment, we then must predict the future trend in glass eel recruitment. There are several possible scenarios for future trends. With the implementation of Eel Management Plans throughout Europe in 2009 and 2010, it is hoped that silver eel escapement will increase, leading to higher spawning stock biomass and thus higher levels of recruitment to European waters. Measures to control silver eel mortality will have an immediate impact on silver eel escapement at the river basin level. Given the typical 5-30 year generation time across European waters, however, measures to reduce mortality and increase production of yellow eels may not yield increased silver eel escapement for many years. Thus, recruitment could continue at very low levels or even decline further for many years before the full benefits of recent management measures across Europe are realised. This range of recruitment projections can be summarised within the following three scenarios:

1. No change;
2. Continued decline for one generation (15 years) followed by gradual increase;
3. Gradual increase.

For the purposes of this report, we will use scenario 2. SMEP II provides two reference recruitment trends (see 5.3.2), representing 1) the average recruitment decline across Europe, and 2) the decline in CPUE of the UK glass eel fishery. The reverse of these trends is also provided in the **ReverseEuropeanRec.csv** and **ReverseUKRecruitment.csv** input files, respectively. Given that the European eel is a single stock, and that impacts and management across all of Europe affect the recovery of silver eel escapement and subsequent recruitment, it may be more appropriate to assume that any recovery of recruitment will be along the lines of the reverse of the European decline rather than the UK trend, which may have been buffered from the European decline to some extent because of the proximity to the edge of the recruitment front. To examine the effects of various anthropogenic impacts, therefore, we have assumed in these projections that recruitment remains low, at 30 per cent of maximum, for 15 years before gradually increasing to 100 per cent over the following 30 years.

It should be noted that some predictions at the level of the whole stock (not using SMEP II) suggest that, even after a complete cessation of all anthropogenic mortalities, full recovery of recruitment might take 80 to 100+ years. Therefore, option 2 applied here may be overly optimistic.

Modelling impacts and comparing management actions

There may be a number of options available to managers to recover silver eel production, depending on the anthropogenic impacts acting on the river basin. For example, there may be fisheries for glass eel in the estuary, and for yellow and silver eels at several locations throughout the basin. Similarly, there might be a number of turbines and water abstractions throughout the basin, and there might be reaches where eel production is limited by poor water quality or where access to eels is impaired. In addition to controls on mortality, managers may have the option to increase local production by stocking eels, or to restore eel-producing habitats by improving water quality or by installing eel passes, and then kick-start eel production by stocking in these additional habitats.

Though the impacts of each of these factors can be considered in isolation, it is more likely that management controls will have to be implemented to reduce the impacts of several factors. Clearly, therefore, the manager may require model simulations with all possible permutations combining the various impacts and inputs (restore habitat, stocking). Here, we limit our consideration to the removal of individual fisheries or a turbine; removing all anthropogenic mortalities at the same time; stocking in an existing reach; restoring and stocking an additional reach; and applying all the measures at the same time.

Although we have noted above that anthropogenic impacts on the glass eel, elver and yellow eel stages are implicit in the observed yellow eel stock, we have simulated a range of these impacts explicitly in the following examples to illustrate the effects of their control on silver eel escapement. For the baseline simulation, we model a yellow eel fishery in Reach 4 that catches 100kg (1,000 eels) per annum, and we apply the silver eel fishery and the turbine mortality, as described above.

Results

Managing mortality impacts

The starting point of recruitment for the baseline scenario was 30 per cent of the maximum, which was lower than the 900,000 or 0.33 of maximum determined above. As a consequence of this, and despite the removal of a yellow eel fishery, silver eel production drops for the first seven years by number (Figure 5.23) and biomass (Figure 5.24). Recruitment begins to increase in year 15 but this is not reflected in increased silver eel production until around year 26, and the escapement biomass has still not reached the 40 per cent target (1,330 kg) by the end of the 45 year simulation (Figure 5.24).

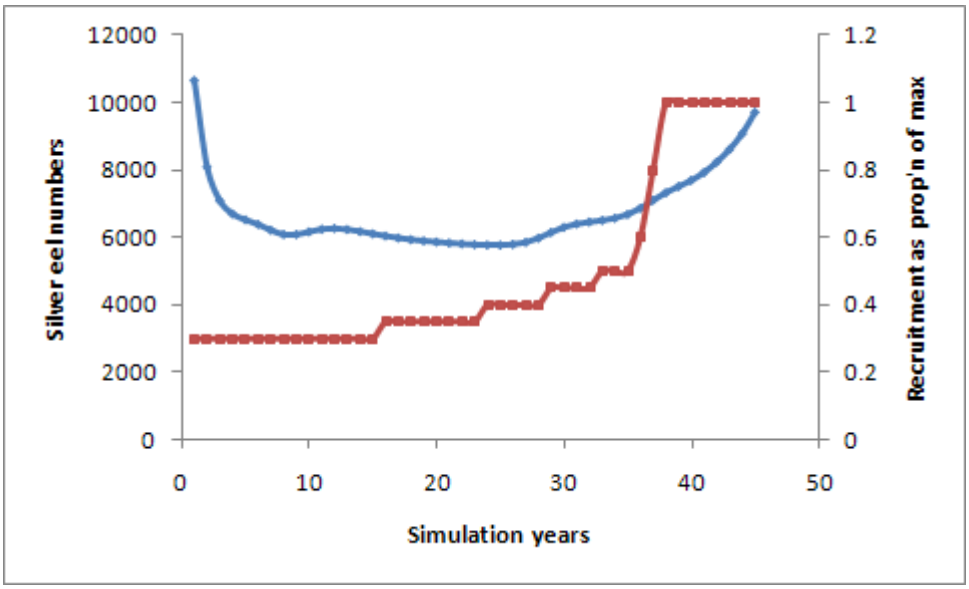

Figure 5.23. Projected trend in silver eel escapement (numbers: blue line) from the baseline condition with yellow and silver eel fisheries and turbine mortality, and trend in recruits (red line) as a proportion of the maximum stable recruitment level.

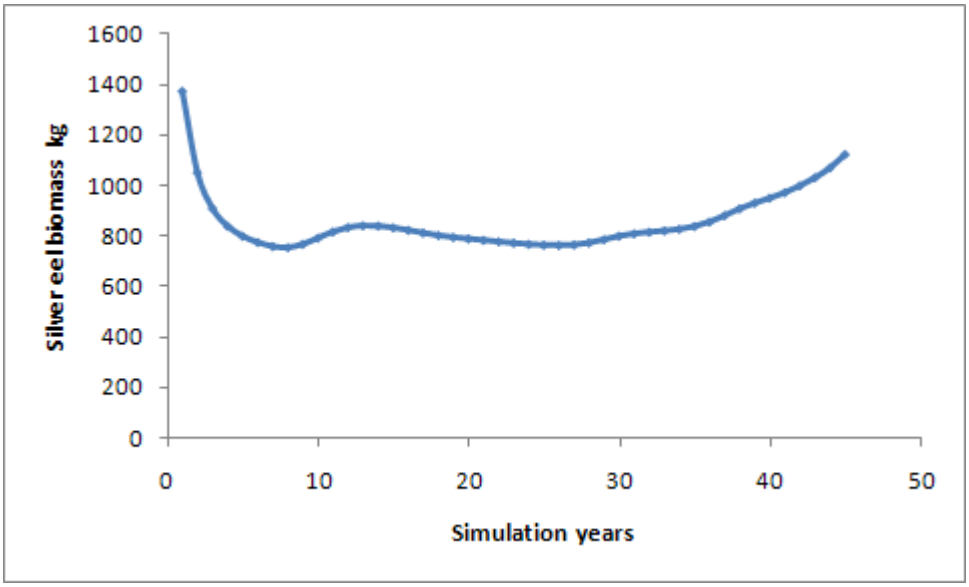

Figure 5.24. Projected trend in silver eel production (biomass: blue line) from the baseline condition with yellow and silver eel fisheries and turbine mortality.

As one would expect, removal of the silver eel fishery and/or the turbine in year 4 has a direct and immediate effect on silver eel escapement, but the effect is relatively small and does little to increase silver eel escapement above the baseline in terms of numbers (Figure 5.25) or biomass of silver eels (Figure 5.26). In contrast, the closure of the yellow eel fishery has a substantial effect on both numbers and biomass of silver eel production, albeit initially delayed by 5 years as one would expect given the average time required for the 'saved' yellow eels to become silver eels.

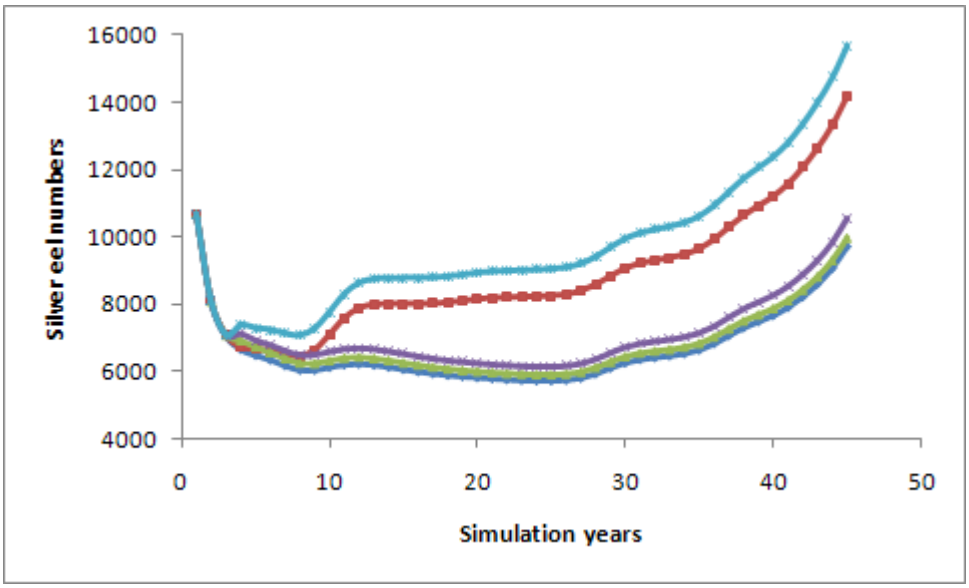

Figure 5.25. Projected trend in silver eel production (numbers) over 45 years with recruitment increasing from years 15 to 45 (as Figure 5.23). The baseline production with no control of fishing or turbine mortalities is shown by the dark blue line. The effects of closing the yellow or silver eel fishery, removing the turbine mortality or removing all mortalities from year 4 onwards are shown by the red, green, purple and pale blue lines, respectively.

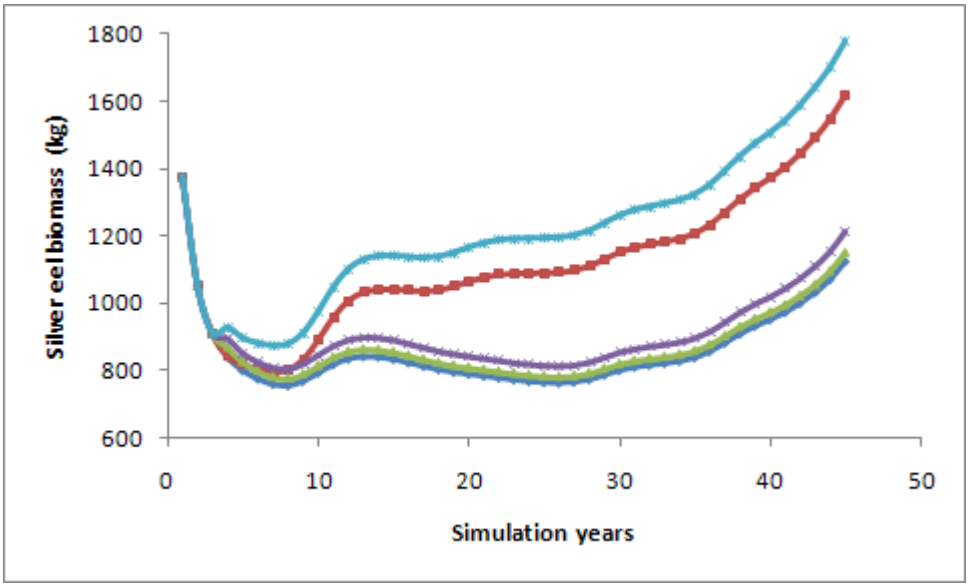

Figure 5.26. Projected trend in silver eel production (biomass, kg) over 45 years with recruitment increasing from years 15 to 45 (as Figure 5.23). The baseline production with no control of fishing or turbine mortalities is shown by the dark blue line. The effects of closing the yellow or silver eel fishery, removing the turbine mortality or removing all mortalities from year 4 onwards are shown by the red, green, purple and pale blue lines, respectively.

Enhancing production through stocking

Although closure of the yellow eel fishery would appear to contribute most in restoring escapement above the management target within the 45 years simulated here, this is dependent on the modelled increase in recruitment. Thus, even removing all anthropogenic mortalities would not be sufficient to achieve compliance in the absence of an 'indirect' increase in recruitment, which will only come from successful management actions in many more river basin districts across Europe. The managers of our river basin may therefore be required to supplement eel production by stocking and/or restoring previously unproductive habitats. Here we illustrate the potential benefits of stocking 20kg (about 60,000) glass eels in the upper parts of the river basin (Reach 15). Given the high price of glass eel for stocking, we assume that stocking is only possible every second year and that it only occurs on five occasions, in years 5, 7, 9, 11 and 13.

Stocking at this level results in only a very small increase in numbers (Figure 5.27) or biomass (Figure 5.28) of silver eel, with similar results regardless of whether other mortalities are removed or allowed to continue.

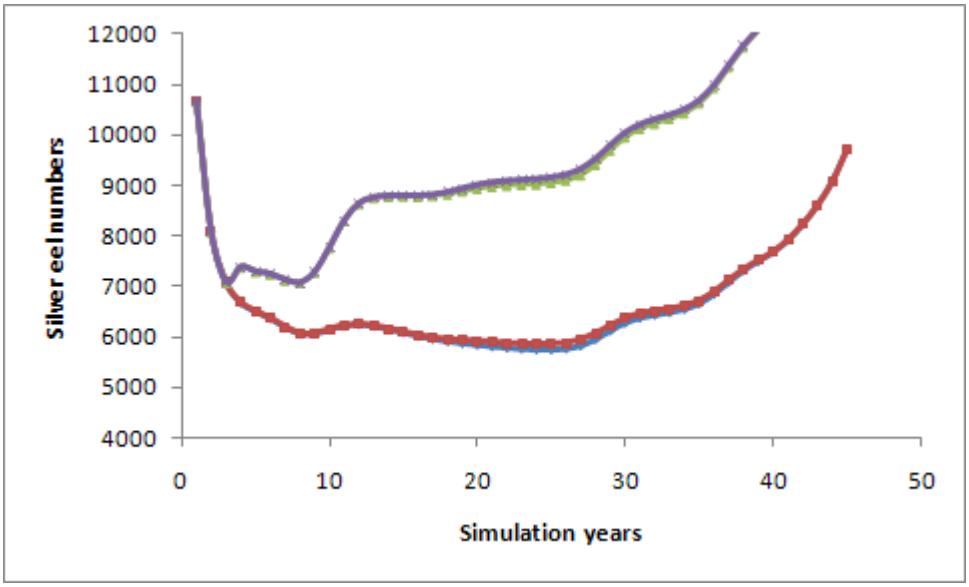

Figure 5.27. Projected trend in silver eel production (numbers) over 45 years with recruitment increasing from years 15 to 45 (as Figure 5.23). The baseline production with no control of fishing or turbine mortalities is shown by the blue line. The effects of stocking in Reach 15 in years 5, 7, 9, 11 and 13 while continuing the fishing and turbine mortalities is shown as the red line, compared to removing all mortalities from year 4 onwards (green) and stocking Reach 15 in each of these years (purple).

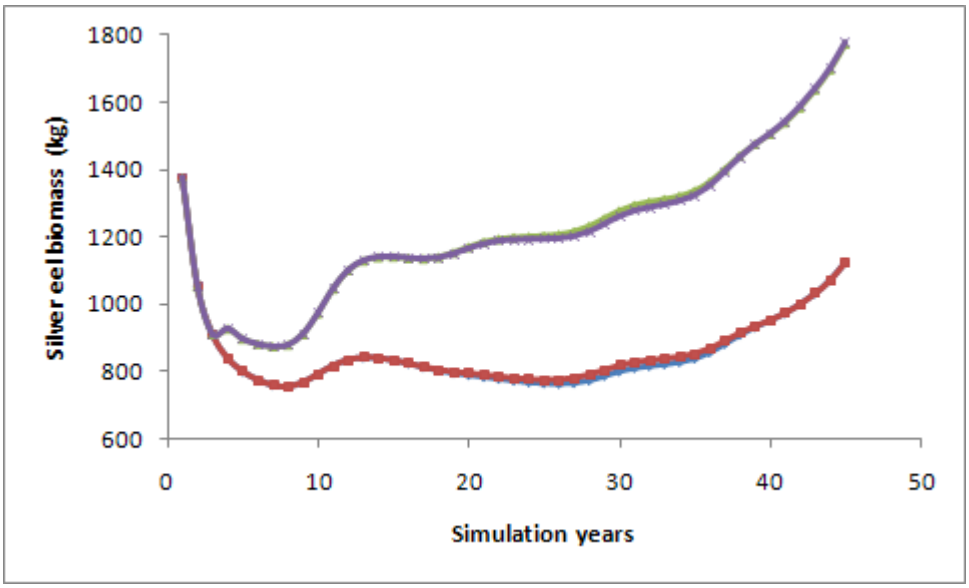

Figure 5.28. Projected trend in silver eel production (biomass, kg) over 45 years with recruitment increasing from years 15 to 45 (as Figure 5.23). The baseline production with no control of fishing or turbine mortalities is shown by the blue line. The effects of stocking in Reach 15 in years 5, 7, 9, 11 and 13 while continuing the fishing and turbine mortalities is shown as the red line, compared to removing all mortalities from year 4 onwards (green) and stocking Reach 15 in each of these years (purple).

Thus, supplementary stocking at this level has little effect on achieving compliance. The market price for glass eel in 2010 was in the region of £600 per kilogramme and therefore the 20kg stocked would have cost £12,000 per annum – a total cost of £60,000 over the 10 years of the stocking programme.

Cost-benefit analysis

This consideration of the cost of stocking in light of the apparently poor return in silver eels illustrates how SMEP II can be used to conduct cost-benefit analyses to compare the effects of various management options. However, as the costs of the various options will be largely determined on a case-by-case basis, it is not possible to provide such a cost-benefit analysis within this report.

5.3.3 Establishing intermediate (or proxy) indicators

The Regulation requires Member States to monitor their eel stocks and report progress towards achieving their management targets. In the absence of the facilities and/or resources to directly monitor silver eel escapement as the measure of achievement or compliance, the Environment Agency must use other measures that are proxies for the silver eel escapement. Proxies could be measures of glass eel and/or elver recruitment to the river basins, or measures of the yellow eel population in the river basins.

Given the panmictic nature of the European eel population, recruitment will be affected by the success of management measures much further afield than the river basin in question, and recruitment to a river is no reflection of the silver eel escapement of that

river. Thus, proxies based on recruitment will be of no use to the Environment Agency, though they will be useful for stock-wide assessments of the status of the European eel.

As noted above, significant practical difficulties apply to the direct quantification of the silver eel escapement, and hence the requirement for assessment models such as SMEP II.

Given that the Environment Agency already conducts eel-specific and multi-species surveys in most river basins of England and Wales, measures of the local yellow eel population will provide the most practical indication of changes in local stock status that can be attributed to management measures implemented by the Environment Agency.

Yellow eel proxies are most likely to be based on the density and/or biomass at select sites throughout the river basin.

As the model outputs include a comprehensive description of the yellow eel population over time, SMEP II can be used to identify target levels based on the yellow eel population, and to predict changes in these proxy indicators. The Environment Agency can then measure these proxies over time to compare with the model predictions. It is important to note that the model predictions will most probably alter as more data become available from surveys of yellow eel populations, and as other studies improve our understanding of eel life history processes. Assessing local stock compliance against proxy indicators will, therefore, be an iterative process.

6 Recommendations for further research and development

6.1 Introduction

We have identified in previous chapters a number of gaps in our understanding of the life history and behaviour of eels that limit our ability to simulate eel production, and gaps in available data on which to test and apply SMEP II. We repeat and expand on these gaps in this chapter. Some references are made to select scientific and grey literature where appropriate, but these are not intended to be comprehensive. There are many gaps in our knowledge and the following is not intended to identify them all, but to select some that are particularly relevant to the further development, testing and application of stock assessment models such as SMEP II.

6.2 Knowledge and understanding of eel life history processes

6.2.1 Natural mortality rates

Mortality is the loss of eels from the population, and can be due to a variety of factors, both natural (chiefly predation, diseases and parasites), and anthropogenic, such as that due directly to fishing, turbines, and so on, or indirectly due to increasing density-dependent mortality because of raising densities below dams and weirs. There are few quantitative studies on mortality rates in eel populations because of the difficulty in actually measuring it in the wild (Knights *et al.*, 1996, 2001). It is assumed from general principles of fish biology that natural mortality will be influenced by density, but there is little information available to prove, let alone quantify, this relationship. Given the difficulties in measuring natural mortality of eels *in situ*, it is hardly surprising that few studies have attempted this or even to explore whether it is the density of eels *per se* that matters or density of particular size classes that are utilising particular niches.

There remains an urgent requirement to quantify rates of natural mortality in glass, yellow and silver eel stages. Further to studies of the general principles, we also must understand how mortality rates are affected by local environments and intra-, and inter-specific competition.

Stocking

Stocking is listed as one management option in the EU Regulation to supplement weakened stocks, or even replace lost ones, as an aid to achieving the long-term silver eel escapement targets. It is essential to optimise the quality and survival of the glass eel destined for stocking, and to stock the eel in habitats that maximise the chance of them contributing to the silver eel escapement. Despite several reviews of eel stocking, there is a lack of information on the outcome of previous stocking exercises in terms survival of stocked material through to eventual escapement of silver eels, both for the stocked eels and in comparison with local stocks of 'wild' eels. Long-term, field-based studies of the survival of 'wild' versus stocked glass eel are required, in conjunction with studies to compare natural mortality rates in donor eel stocks and those of stocked eels.

6.2.2 Sex differentiation

The biological mechanism by which individual eels become male or female is not well understood (Davey and Jellyman, 2005). The sex of developing gonads is labile and gender is determined principally by environmental factors, occurring at some early stage in the growth phase of the yellow eel. Trends in the relative production of male versus female eels have been variously linked to differences in habitat, thermal regime, population density, growth rate and food availability, all of which may be interrelated to some extent.

The absence of a non-destructive method of determining the sex of individuals means that it is very difficult to know when differentiation is initiated, and therefore what environmental conditions result in an individual becoming male or female. Given that eels may spend more than 10 years in a river (and females could spend much longer than that), and could differentiate during the first few years in the river, there might be a gap of several years, and opportunity for considerable movement, between the time when the eels differentiated and when density is measured at time of sampling. Thus, the conditions at the time of sampling might bear no resemblance to the conditions when differentiation to one or other gender was initiated.

Research is required to understand what factors influence sex determination, when and where these factors occur, and to develop non-destructive methods to provide direct quantification of sex ratios at survey sites rather than relying on pooled whole-river data based on few samples per site.

6.2.3 Environment influences on eel production

Production of eel may be influenced by direct mechanisms on the processes and the eel population, or by indirect mechanisms acting on the inputs to the population (that is, recruitment) by virtue of the location and physical characteristics of the habitat. The carrying capacity of a system, whether it is a river reach, an estuary or a river basin, should be linked to the productivity of a water body, with the more productive habitats having a higher carrying capacity that sustains a greater biomass.

Although we have measures of eel numbers and biomass at an increasing number of survey sites and from an increasing variety of local habitat conditions, knowledge of a

quantifiable relationship between habitat and eel production is still lacking and research is required to address this, both for production in freshwater and saline environments.

6.2.4 Factors stimulating effects of density

A recurring theme throughout this report and chapter is that though it appears to be an important force, we have a limited understanding of how density affects the biology and dynamics of eels. In addition to quantifying the effects of density on life history of eel, we must understand the fundamental mechanisms that drive these changes. For example, given that growth is likely to be resource-limited, it is reasonable to assume that there may be an effect of density on growth rates. However, it is difficult to quantify a density-dependent effect in the natural environment because of fluctuations in local populations and environmental conditions. Few studies have even considered evidence for such an effect, let alone attempted to quantify the relationship between density and growth.

Research is required to address a number of questions including:

- What is the competition mechanism stimulating this effect?
- Is it direct competition for resources (food, space) or is it indirect effects such as contact, or both?
- Is it only eels within a certain size range relative to the affected individual that have an influence? And in such cases does the threshold vary between sizes of eels?
- Is it only the presence of other eels or does the presence of other fish species, invertebrates, and so on, matter?

6.3 Knowledge and understanding of eel behaviour

The process of dispersal of eels throughout river basins appears to be driven by two mechanisms, corresponding to density-dependent situations and an inherent tendency to move upstream. Although a number of tracking and mark-recapture studies have been reported, the literature provides no direct measures of stage-specific rates at which eels disperse throughout river systems, let alone comparisons between rates at different densities. Research is required to quantify these dispersal rates in relation to variations in eel density and environmental factors.

Potential obstructions to eel passage exist in many (perhaps most) river basins in England and Wales. The obvious obstructions are in-stream structures like weirs and dams, but large bodies of standing water may act as a ‘sink’ for eels, slowing their upstream dispersal. At present we have little knowledge of the obstructive nature of in-stream structures or standing waters and therefore it is very difficult to model their potential effects. In addition, we do not understand the subsequent effects on individual eels and local stocks of a concentration of eels below significant barriers to their movement. It is reasonable to assume that such concentrations might result in increased competition for resources and increased mortality rates, either from insufficient resources or attraction of predators, but perhaps eels avoid this by moving

downstream away from the barrier. Clearly there are several large gaps in our knowledge in the process of dispersal of eels, and these need to be addressed.

6.4 Model testing

Ideally, SMEP II should be tested on data scenarios that provide annual numbers of total recruits (glass eels and/or settled elvers), a comprehensive survey dataset of the yellow eel population with survey sites located throughout the basin covering all habitat types, and annual counts and weights of silver eels escaping from the lowermost point of the study basin. In addition, there should be comprehensive data on individual growth rates, sex ratio at each survey location, and rates of natural and anthropogenic mortalities. Unfortunately, such an ideal, data-rich scenario is not available from river basins in England and Wales, or throughout the UK.

The EU-funded *Pilot projects to estimate actual and potential silver eel escapement* (POSE) is addressing this requirement to test eel assessment models against data-rich and data-poor scenarios, and to develop a framework with which to apply model results to basins where no eel data are available. SMEP II is included within the suite of assessment models tested in POSE against river basins from across Europe with different elements of data-richness. POSE will provide a significant validation of SMEP II which has not been possible for rivers in England and Wales due to the lack of river basins with comprehensive data on eel.

6.5 Model application

6.5.1 Quantify recruitment and settlement

A measure of recruitment of eels to the study river is required where a simulation occurs over a number of years. It is important to recognise that the ‘recruitment’ modelled is the income of eels to the study area, and not necessarily the amount of glass eel entering an estuary. If the study area includes an estuary, then recruitment will mean the amount of glass eel entering the estuary from the sea. However, if the study area begins upstream of the estuary then the modelled recruitment may be the quantity of eels that transform from glass eels to elvers, that is, those that ‘settle’.

There are very few examples of measured recruitment or settlement for the UK or across Europe, and research is required to establish baseline data for both eel stages and for index river basins representing different recruitment regimes, that is, west coast versus east coast.

6.5.2 Characterise the existing yellow eel population

The method developed in this report to model extant silver eel escapement from the study basin requires data on the yellow eels collected from surveys distributed

throughout the river basin. However, it is very unlikely that surveys will be possible in all habitats and across the entire river basin, because of the practical difficulties in collecting quantitative measures of local eel production in saline and/or deep waters, and because of resource limits. Therefore, the method requires an extrapolation of yellow eel data from survey sites to the associated reaches and beyond. A much greater understanding of the relationships between eel production and habitats (see above) is required in order to develop the extrapolation beyond the simple linear form used in this project. Furthermore, and especially given the resource limits, research is required to establish the optimum yellow eel survey design, in terms of numbers and distribution of sites

References

ACOU, A., BOURY, P., LAFFAILLE, P., CRIVELLI, A. J. AND FEUNTEUN, E. (2005). Towards a standardized characterization of the potentially migrating silver European eel (*Anguilla anguilla*, L.). *Archiv fur Hydrobiologie* 164, 237-255.

ACOU, A., GABRIEL, G., LAFFAILLE, P. AND FEUNTEUN, E. (2009). Differential production and condition indices of premigrant eels (*Anguilla anguilla*) in two small Atlantic coastal catchments of France. In *Eels at the Edge: Science, Status, and Conservation Concerns* (Casselmon, J. H. and Cairns, D. K., eds.), pp. 157-174. American Fisheries Society Symposium 58: Bethesda, Maryland, USA.

ACOU, A., LEFEBVRE, F., CONTOURNET, P., POIZAT, G., PANFILI, J. AND CRIVELLI, A. J. (2003). Silvering of female eels (*Anguilla anguilla*) in two sub-populations of the Rhone delta. BFPP. *Bulletin Francais de la Peche et de la Protection des Milieux Aquatiques*, 55-68.

APRAHAMIAN, M. W. (1986). Eel (*Anguilla anguilla* L.) production in the River Severn, England. *Polskie Archiwum Hydrobiologii,* 33, 373-389.

APRAHAMIAN, M. W. (1988). Age structure of eel, *Anguilla anguilla* (L.), populations in the River Severn, England, and the River Dee, Wales. *Aquaculture and Fisheries Management* 19, 365-376.

APRAHAMIAN, M. W. (2000). The growth rate of eel in tributaries of the lower River Severn, England, and its relationship with stock size. *Journal of Fish Biology* 56, 223-227.

APRAHAMIAN, M. W., WALKER, A. M., WILLIAMS, B., BARK, A. AND KNIGHTS, B. (2007). On the application of models of European eel (*Anguilla anguilla*) production and escapement to the development of Eel Management Plans: the River Severn. *ICES Journal of Marine Science* 64, 1472-1482.

ARAI, T., KOTAKE, A., LOKMAN, P. M., MILLER, M. J. AND TSUKAMOTO, K. (2004). Evidence of different habitat use by New Zealand freshwater eels Anguilla australis and A. dieffenbachii, as revealed by otolith microchemistry. *Marine Ecology Progress Series* 266, 213-225.

ARAI, T., KOTAKE, A. AND MCCARTHY, T. K. (2006). Habitat use by the European eel *Anguilla anguilla* in Irish waters*. Estuarine, Coastal and Shelf Science* 67, 569-578.

BARAK, N. A. E. AND MASON, C. F. (1992). Population density, growth and diet of eels, *Anguilla anguilla* L., in two rivers in eastern England. *Aquaculture and Fisheries Management* 23, 59-70.

BARAS, E., JEANDRAIN, D., SEROUGE, B. AND PHILIPPART, J. C. (1998). Seasonal variations in time and space utilization by radio-tagged yellow eels *Anguilla anguilla* (L.) in a small stream. *Hydrobiologia* 371-372, 187-198.

BARK, A., KNIGHTS, B., WILLIAMS, B., KIRKWOOD, G., AND EL- HOSAINI, H. (2007). Development and implementation of Biological Reference Points for the management of the European eel (Anguilla anguilla L.) DEFRA report SFO 236.

BARK, A., WILLIAMS, B. AND KNIGHTS, B. (2007). Current status and temporal trends in stocks of European eel in England and Wales. *ICES Journal of Marine Science* 64, 1368-1378.

BARK, A., WILLIAMS, B. AND KNIGHTS, B. (2009). Long-term changes in recruitment, population dynamics, and the status of the European eel in two English river systems. In *Eels at the Edge: Science, Status, and Conservation Concerns* (Casselman, J. M. and Cairns, D. K., eds.), pp. 241-256. American Fisheries Society Symposium 58: Bethesda, Maryland, USA.

BEAULATON, L. AND BRIAND, C. (2007). Effect of management measures on glass eel escapement. *ICES Journal of Marine Science* 64, 1402-1413.

BEVACQUA, D., MELIA, P., CRIVELLI, A. J., DE LEO, G. A. AND GATTO, M. (2006). Timing and rate of sexual maturation of European eel in brackish and freshwater environments. *Journal of Fish Biology* 69, 200-208.

BEVACQUA, D., MELIA, P., CRIVELLI, A. J., GATTO, M. AND DE LEO, G. A. (2007). Multi-objective assessment of conservation measures for the European eel (Anguilla anguilla): an application to the Camargue lagoons. *ICES Journal of Marine Science* 64, 1483-1490.

BEVERTON, R. J. H. AND HOLT, S. J. (1957). On the dynamics of exploited fish populations: Ministry of Agriculture, Fisheries and Food, UK.

BISGAARD, J. AND PEDERSON, M. I. (1991). Mortality and growth of wild and introduced cultured eels (*Anguilla anguilla* (L.)) in a Danish stream, with special reference to a new tagging technique. *Dana* 9, 57-69.

BRIAND, C., FATIN, D., FONTENELLE, G. AND FEUNTEUN, E. (2003). Estuarine and fluvial recruitment of the European glass eel, *Anguilla anguilla*, in an exploited Atlantic estuary. *Fisheries Management and Ecology* 10, 377-384.

BROAD, T. L., TOWNSEND, C. R., ARBUCKLE, C. J. AND JELLYMAN, D. J. (2001). A model to predict the presence of longfin eels in some New Zealand streams, with particular reference to riparian vegetation and elevation. *Journal of Fish Biology* 58, 1098-1112.

CARSS, D. N., ELSTON, D. A., NELSON, K. C. AND KRUUK, H. (1999). Spatial and temporal trends in unexploited yellow eel stocks in two shallow lakes and associated streams. *Journal of Fish Biology* 55, 636-654.

CHADWICK, S., KNIGHTS, B., THORLEY, J. L. AND BARK, A. (2007). A long-term study of population characteristics and downstream migrations of the European eel *Anguilla anguilla* (L.) and the effects of a migration barrier in the Girnock Burn, north-east Scotland. *Journal of Fish Biology* 70, 1535-1553.

CULLEN, P. AND MCCARTHY, T. K. (2003). Hydrometric and meteorological factors affecting the seaward migration of silver eels (*Anguilla anguilla*, L.) in the lower River Shannon. *Environmental Biology of Fishes* 67, 349-357.

DAVERAT, F., ELIE, P. AND LAHAYE, M. (2004). Microchemistry contribution to a first approach to the diversity of life histories of eels from the lower part of the Gironde-Garonne-Dordogne watershed. *Cybium* 28, 83-90.

DAVERAT, F., LIMBURG, K. E., THIBAULT, I., SHIAO, J.-C., DODSON, J. J., CARON, F., TZENG, W.-N., IIZUKA, Y. AND WICKSTROM, H. (2006). Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. *Marine Ecology Progress Series* 308, 231-241.

DAVERAT, F. AND TOMAS, J. (2006). Tactics and demographic attributes in the European eel *Anguilla anguilla* in the Gironde watershed, SW France. *Marine Ecology Progress Series* 307, 247-257.

DAVEY, A. J. H. AND JELLYMAN, D. J. (2005). Sex determination in freshwater eels and management options for manipulation of sex. *Reviews in Fish Biology and Fisheries* 15, 37-52.

DE LEO, G. A. AND GATTO, M. (1995). A size and age-structured model of the European eel (*Anguilla anguilla* L.). *Canadian Journal of Fisheries & Aquatic Sciences* 52, 1351-1367.

DE LEO, G. A. AND GATTO, M. (1996). Trends in vital rates of the European eel: evidence for density dependence? *Ecological Applications* 6, 1281-1294.

DEELDER, C. L. (1984). Synopsis of biological data on the eel, *Anguilla anguilla* (Linnaeus, 1758). In *FAO Fisheries Synopsis*, 80, Revision 1, p. 73.

DEKKER, W. (2000). The fractal geometry of the European eel stock*. ICES Journal of Marine Science* 57, 109-121.

DEKKER, W., PAWSON, M., WALKER, A. M., ROSELL, R., EVANS, D., BRIAND, C., CASTELNAUD, G., LAMBERT, P., BEAULATON, L., ASTROM, M., WICKSTROM, H., POOLE, R., MCCARTHY, T. K., BLASZKOWSKI, M., DE LEO, G. A. AND BEVACQUA, D. (2006). Restoration of the European eel population; pilot studies for a scientific framework in support of sustainable management: SLIME. In *EU Sixth Framework Programme*, Priority 8.1, Policy-orientated research, Scientific Support to Policies, p. 19.

DURIF, C., DUFOUR, S. AND ELIE, P. (2005). The silvering process of *Anguilla anguilla*: A new classification from the yellow resident to the silver migrating stage. *Journal of Fish Biology* 66, 1025-1043.

EDELINE, E., LAMBERT, P., RIGAUD, C. AND ELIE, P. (2006). Effects of body condition and water temperature on *Anguilla anguilla* glass eel migratory behavior. Journal of Experimental Marine Biology and Ecology 331, 217-225.

ELIE, P. AND DAGUZAN, J. (1976). Alimentation et croissance des civelles d'Anguilla anguilla L. (poisson Teleosteen Anguilliforme) elevees experimentalement a diverses temperatures au laboratoire. *Extrait des Annales de la Nutrition et de l'Alimentation* 30, 95-114.

FEUNTEUN, E. (2002). Management and restoration of European eel population (Anguilla anguilla): An impossible bargain. *Ecological Engineering* 18, 575-591.

FEUNTEUN, E., ACOU, A., LAFFAILLE, P. AND LEGAULT, A. (2000). European eel (Anguilla anguilla): Prediction of spawner escapement from continental population parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 1627-1635.

FEUNTEUN, E., LAFFAILLE, P., ROBINET, T., BRIAND, C., BAISEZ, A., OLIVIER, J. M. AND ACOU, A. (2003). A Review of Upstream Migration and Movements in Inland Waters by Anguillid Eels: Toward a General Theory. In *Eel Biology* (Aida, K., Tsukamoto, K. and Yamauchi, K., eds.), pp. 191-213. Tokyo: Springer- Verlab.

FRANCIS, R. I. C. C. AND JELLYMAN, D. J. (1999). Are mean size data adequate to monitor freshwater eel fisheries? *Marine and Freshwater Research* 50, 355-366.

HAN, Y.-S. AND TZENG, W.-N. (2006). Use of the sex ratio as a means of resource assessment for the Japanese eel Anguilla japonica: A case study in the Kaoping River, Taiwan. *Zoological Studies* 45, 255-263.

HOLMGREN, K. AND MOSEGAARD, H. (1996). Implications of individual growth status on the future sex of the European eel. *Journal of Fish Biology* 49, 910-925.

HOLMGREN, K., WICKSTROM, H. AND CLEVESTAM, P. (1997). Sex-related growth of European eel, *Anguilla anguilla*, with focus on median silver eel age. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 2775-2781.

HUERTAS, M. AND CERDA, J. (2006). Stocking density at early developmental stages affects growth and sex ratio in the European eel (*Anguilla anguilla*). *Biological Bulletin* 211, 286-296.

HUSSEIN, S. A. (1981). The population density, growth and food of eels *Anguilla anguilla* (L.) in some tributaries of the River Tweed. In *2nd British Freshwater Fisheries Conference*, pp. 120-128. Liverpool: University of Liverpool Press.

HVIDSTEN, N. A. (1985). Ascent of elvers (*Anguilla anguilla* L.) in the Stream Imsa, Norway. Report of the Institute of Freshwater Research, Drottningholm 62, 71-74.

IBBOTSON, A., SMITH, J., SCARLETT, P. AND APRAHAMIAN, M. (2002). Colonisation of freshwater habitats by the European eel *Anguilla anguilla*. *Freshwater Biology* 47, 1696-1706.

International Council for the Exploration of the Seas (2006). Report of the 2006 session of the Joint EIFAC/ICES Working Group on Eels, Rome, Italy, 23-27 January 2006. EIFAC Occasional Paper. No. 38, ICES CM 2006/ACFM:16, 352 pp.

International Council for the Exploration of the Seas (2001). Report of the 2000 session of the Joint EIFAC/ICES Working Group on Eels, St. Andrews, New Brunswick, Canada. In ICES CM 2001/ACFM:03, p. 91.

International Council for the Exploration of the Seas (2007). Report of the 2007 session of the Joint EIFAC/ICES Working Group on Eels, Bordeaux, France. In EIFAC Occasional Paper. No. 39, ICES CM 2007/ACFM:23, p. 138. Rome, FAO/Copenhagen, ICES.

International Council for the Exploration of the Seas (2008). Report of the 2008 session of the Joint EIFAC/ICES Working Group on Eels, Leuven, Belgium. In EIFAC Occasional Paper No. 43. ICES CM 2009/ACOM:15, p. 192. Rome, FAO/Copenhagen, ICES.

International Council for the Exploration of the Seas (2010). Report of the 2010 session of the Joint EIFAC/ICES Working Group on Eels, Hamburg, Germany. In EIFAC Occasional Paper No. 41. ICES CM 2010/ACOM:18, 721 pp. Rome, FAO/Copenhagen, ICES.

JELLYMAN, D. J. (1997). Variability in growth rates of freshwater eels (*Anguilla* spp.) in New Zealand. *Ecology of Freshwater Fish* 6, 108-115.

JELLYMAN, D. J. (2001). The influence of growth rate on the size of migrating female eels in Lake Ellesmere, New Zealand. *Journal of Fish Biology* 58, 725-736.

JESSOP, B. M., SHIAO, J. C., IIZUKA, Y. AND TZENG, W. N. (2004). Variation in the annual growth, by sex and migration history, of silver American eels *Anguilla rostrata*. *Marine Ecology Progress Series* 272, 231-244.

KLEIN BRETELER, J., VRIESE, T., BORCHERDING, J., BREUKELAAR, A., JORGENSEN, L., STAAS, S., DE LAAK, G. AND INGENDAHL, D. (2007). Assessment of population size and migration routes of silver eel in the River Rhine based on a 2-year combined mark-recapture and telemetry study. *ICES Journal of Marine Science* 64, 1450-1456.

KNIGHTS, B., BARK, T. AND WILLIAMS, B. (2001). Eel and elver stocks in England and Wales: status and management options. p. 317. Bristol: Environment Agency.

KNIGHTS, B., WHITE, E. AND NAISMITH, I. A. (1996). Stock assessment of European eel, *Anguilla anguilla* L. In *Stock Assessment in Inland Fisheries* (Cowx, I. C., ed.), pp. 431-447. Oxford: Blackwell Science Ltd.

KRUEGER, W. H. AND OLIVEIRA, K. (1999). Evidence for environmental sex determination in the American eel, *Anguilla rostrata*. *Environmental Biology of Fishes* 55, 381-389.

LAFFAILLE, P., ACOU, A. AND GUILLOUET, J. (2005). The yellow European eel (Anguilla anguilla L.) may adopt a sedentary lifestyle in inland freshwaters. *Ecology of Freshwater Fish* 14, 191-196.

LAMBERT, P. AND ROCHARD, E. (2007). Identification of the inland population dynamics of the European eel using pattern-oriented modelling. *Ecological Modelling* 206, 166-178.

LAMSON, H. M., CAIRNS, D. K., SHIAO, J. C., IIZUKA, Y. AND TZENG, W. N. (2009). American eel, *Anguilla rostrata*, growth in fresh and salt water: implications for conservation and aquaculture. *Fisheries Management and Ecology* 16, 306-314.

LARINIER, M. AND TRAVADE, F. (2002). Downstream migration: problems and facilities. *Bulletin de la Societe Zoologique de France* 364 supplement, 181-207.

LASNE, E. AND LAFFAILLE, P. (2008). Analysis of distribution patterns of yellow European eels in the Loire catchment using logistic models based on presence-absence of different size-classes. Ecology of Freshwater *Fish* 17, 30-37.

LIN, Y. J., LOZYS, L., SHIAO, J. C., IIZUKA, Y. AND TZENG, W. N. (2007). Growth differences between naturally recruited and stocked European eel *Anguilla anguilla* from different habitats in Lithuania. *Journal of Fish Biology* 71, 1773-1787.

LOBON-CERVIA, J. AND IGLESIAS, T. (2008). Long-term numerical changes and regulation in a river stock of European eel *Anguilla anguilla*. *Freshwater Biology* 53, 1832-1844.

LOBON-CERVIA, J., UTRILLA, C. G. AND RINCON, P. A. (1995). Variations in the population dynamics of the European eel *Anguilla anguilla* (L.) along the course of a Cantabrian river. *Ecology of Freshwater Fish* 4, 17-27.

MANN, R. H. K. AND BLACKBURN, J. H. (1991). The biology of the eel *Anguilla anguilla* (L.) in an English chalk stream and interactions with juvenile trout *Salmo trutta* L. and salmon *Salmo salar* L. *Hydrobiologia* 218, 65-76.

MELIA, P., BEVACQUA, D., CRIVELLI, A. J., DE LEO, G. A., PANFILI, J. AND GATTO, M. (2006a). Age and growth of *Anguilla anguilla* in the Camargue lagoons. *Journal of Fish Biology* 68, 876-890.

MELIA, P., BEVACQUA, D., CRIVELLI, A. J., PANFILI, J., DE LEO, G. A. AND GATTO, M. (2006b). Sex differentiation of the European eel in brackish and freshwater environments: A comparative analysis. *Journal of Fish Biology* 69, 1228-1235.

MORIARTY, C. (1986). Riverine migration of young eels *Anguilla anguilla* (L.). *Fisheries Research* 4, 43-58.

MORIARTY, C. (2003). The Yellow Eel. In *Eel Biology* (Aida, K., Tsukamoto, K. and Yamauchi, K., eds.), pp. 89-105. Tokyo: Springer-Verlab.

NAISMITH, I. A. AND KNIGHTS, B. (1988). Migrations of elvers and juvenile European eels, *Anguilla anguilla* L., in the River Thames. *Journal of Fish Biology* 33, 161-175.

NAISMITH, I. A. AND KNIGHTS, B. (1990). Modelling of unexploited and exploited populations of eels, *Anguilla anguilla* (L.), in the Thames Estuary. *Journal of Fish Biology* 37, 975-986.

NAISMITH, I. A. AND KNIGHTS, B. (1993). The distribution, density and growth of the European eel, *Anguilla anguilla*, in the freshwater catchment of the River Thames. *Journal of Fish Biology* 42, 217-226.

OLIVEIRA, K. AND MCCLEAVE, J. D. (2002). Sexually different growth histories of the American eel in four rivers in Maine. *Transactions of the American Fisheries Society* 131, 203-211.

OLIVEIRA, K., MCCLEAVE, J. D. AND WIPPELHAUSER, G. S. (2001). Regional variation and the effect of lake: River area on sex distribution of American eels. *Journal of Fish Biology* 58, 943-952.

PARSONS, J., VICKERS, K. U. AND WARDEN, Y. (1977). Relationship between elver recruitment and changes in the sex ratio of silver eels *Anguilla anguilla* L. migrating from Lough Neagh, Northern Ireland. *Journal of Fish Biology* 10, 211-229.

PEDERSEN, M. I. (1998). Recapture rate, growth and sex of stocked cultured eels *Anguilla anguilla* (L.). BFPP - *Bulletin Francais de la Peche et de la Protection des Milieux Aquatiques* 71, 153-162.

POOLE, R. W. AND REYNOLDS, J. D. (1996a). Age and growth of yellow eel, Anguilla anguilla (L.), determined by two different methods. *Ecology of Freshwater Fish* 5, 86-95.

POOLE, R. W. AND REYNOLDS, J. D. (1996b). Growth rate and age at migration of *Anguilla anguilla*. *Journal of Fish Biology* 48, 633-642.

POOLE, R. W. AND REYNOLDS, J. D. (1998). Variability in growth rate in European eel *Anguilla anguilla* (L.) in a western Irish catchment. *Proceedings of the Royal Irish Academy - Section B Biology and Environment* 98, 141-145.

QUINN, T. J. AND DERISO, R. B. (1999). *Quantitative Fish Dynamics* (Biological Resource Management Series). Oxford: Oxford University Press.

RASMUSSEN, G. AND THERKILDSEN, B. (1979). Food, growth and production of *Anguilla anguilla* L. in a small Danish stream. *Rapports et Process-Verbaux Conseil International pour l'Exploration du la Mer* 174, 32-40.

REID, K. B. (2001). The decline of American eel (*Anguilla rostrata*) in Lake Ontario/St. Lawrence River ecosystem: a modelling approach to identification of data gaps and research priorities. Ann Arbor, Michigan: Lake Ontario Committee, Great Lakes Fishery Commission.

ROBINET, T., ACOU, A., BOURY, P. AND FEUNTEUN, E. (2007). Concepts for characterizing spawning biomass of the European eel (*Anguilla anguilla*) in catchments. *Vie et Milieu* 57, 201-211.

RONCARATI, A., MELOTTI, P., MORDENTI, O. AND GENNARI, L. (1997). Influence of stocking density of European eel (*Anguilla anguilla*, L.) elvers on sex differentiation and zootechnical performances. *Journal of Applied Ichthyology* 13, 131-136.

ROSELL, R., EVANS, D. AND ALLEN, M. (2005). The eel fishery in Lough Neagh, Northern Ireland - An example of sustainable management? *Fisheries Management and Ecology* 12, 377-385.

SHIAO, J. C., LOZYS, L., IIZUKA, Y. AND TZENG, W. N. (2006). Migratory patterns and contribution of stocking to the population of European eel in Lithuanian waters as indicated by otolith Sr:Ca ratios. *Journal of Fish Biology* 69, 749-769.

SIMON, J. (2007). Age, growth, and condition of European eel (*Anguilla anguilla*) from six lakes in the River Havel system (Germany). *ICES Journal of Marine Science* 64, 1414-1422.

SIMPSON, J. M. AND MCGILCHRIST, C. A. (1980). Growth-variable distribution and mortality. *Mathematical Biosciences* 50, 159-162.

SINHA, V. R. P. AND JONES, J. W. (1967). On the food of the freshwater eels and their feeding relationship with salmonids. *Journal of Zoology* 153, 119-137.

SVEDANG, H. (1999). Vital population statistics of the exploited eel stock on the Swedish west coast. *Fisheries Research* 40, 251-265.

SVEDANG, H., NEUMAN, E. AND WICKSTROM, H. (1996). Maturation patterns in female European eel: Age and size at the silver eel stage. *Journal of Fish Biology* 48, 342-351.

TESCH, F. W. (2003). *The eel*. Oxford: Blackwell Science Ltd.

TSUKAMOTO, K. AND ARAI, T. (2001). Facultative catadromy of the eel *Anguilla japonica* between freshwater and seawater habitats. *Marine Ecology Progress Series* 220, 265-276.

TZENG, W.-N., SHIAO, J.-C., YAMADA, Y. AND OKA, H. P. (2003). Life history patterns of Japanese eel *Anguilla japonica* in Mikawa Bay, Japan. American Fisheries Society Symposium 2003, 285-293.

TZENG, W. N., LIN, H. R., WANG, C. H. AND XU, S. N. (2000). Differences in size and growth rates of male and female migrating Japanese eels in Pearl River, China. *Journal of Fish Biology* 57, 1245-1253.

TZENG, W. N., SEVERIN, K. P. AND WICKSTROM, H. (1997). Use of otolith microchemistry to investigate the environmental history of European eel *Anguilla anguilla*. *Marine Ecology Progress Series* 149, 73-81.

VOLLESTAD, L. A. (1992). Geographic variation in age and length at metamorphosis of maturing European eel: environmental effects and phenotypic plasticity. *Journal of Animal Ecology* 61, 41-48.

VOLLESTAD, L. A. AND JONSSON, B. (1988). A 13-year study of the population dynamics and growth of the European eel *Anguilla anguilla* in a Norwegian river: evidence for density-dependent mortality, and development of a model for predicting yield. *Journal of Animal Ecology* 57, 983-997.

VOLLESTAD, L. A., JONSSON, B., HVIDSTEN, N. A. AND NAESJE, T. F. (1994). Experimental test of environmental factors influencing the seaward migration of European silver eels. *Journal of Fish Biology* 45, 641-651.

WALKER, A. M., APRAHAMIAN, M., GODFREY, J., ROSELL, R. AND EVANS, D. (2009). Report on the eel stock and fishery in the UK 2008/2009. In *Report of the 2009 Session of the Joint EIFAC/ICES Working Group on Eels (WGEEL),* ICES CM 2009/ACOM:15, pp. 504-540: EIFAC/ICES.

WALKER, A. M., APRAHAMIAN, M., GODFREY, J., ROSELL, R. AND EVANS, D. (2010). Report on the eel stock and fishery in the United Kingdom: 2009-2010. In *Report of the 2010 Session of the Joint EIFAC/ICES Working Group on Eels*, p. 57 pp. Hamburg, Germany.

WALSH, C. T., PEASE, B. C. AND BOOTH, D. J. (2004). Variation in the sex ratio, size and age of longfinned eels within and among coastal catchments of south-eastern Australia. *Journal of Fish Biology* 64, 1297-1312.

WALSH, C. T., PEASE, B. C., HOYLE, S. D. AND BOOTH, D. J. (2006). Variability in growth of longfinned eels among coastal catchments of south-eastern Australia. *Journal of Fish Biology* 68, 1693-1706.

WESTIN, L. (2003). Migration failure in stocked eels *Anguilla anguilla*. *Marine Ecology Progress Series* 254, 307-311.

WHITE, E. M. AND KNIGHTS, B. (1997). Dynamics of upstream migration of the European eel, *Anguilla anguilla* (L.), in the Rivers Severn and Avon, England, with special reference to the effects of man-made barriers. *Fisheries Management and Ecology* 4, 311-324.

WHITEHEAD, H. (2000). Density-dependent habitat selection and the modelling of sperm whale (*Physeter macrocephalus*) exploitation. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 223-230.

WINTER, H. V., JANSEN, H. M., ADAM, B. AND SCHWEVERS, U. (2005). Behavioural effects of surgically implanting transponders in European eel, *Anguilla anguilla*. In Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe. Ustica, Italy, 9-13 June 2003. (Spedicato, M. T., Lembo, G. & Marmulla, G., eds.). Rome.

WINTER, H. V., JANSEN, H. M. AND BRUIJS, M. C. M. (2006). Assessing the impact of hydropower and fisheries on downstream migrating silver eel, *Anguilla anguilla*, by telemetry in the River Meuse. *Ecology of Freshwater Fish* 15, 221-228.

Would you like to find out more about us, or about your environment?

Then call us on
08708 506 506* (Mon-Fri 8-6)

email
enquiries@environment-agency.gov.uk

or visit our website
www.environment-agency.gov.uk

incident hotline 0800 80 70 60 (24hrs)
floodline 0845 988 1188

* Approximate call costs: 8p plus 6p per minute (standard landline).
Please note charges will vary across telephone providers

Environment first: This publication is printed on recycled paper.