Executive summary:

Eels play an important socio-economic and ecological role in many European countries. The stock of the European eel (Anguilla anguilla), like those of the Japanese and American eel, has declined dramatically in recent times. Recruitment of glass eels has fallen to below 5% of peak levels and catches of yellow and silver eels have declined from 40,000t in the 1960s to less than 20,000t today. The stock is judged to be outside safe biological limits and the EU's Eel Recovery Plan aims to maximize silver eel production and escapement to the sea to ensure that enough eels reach the spawning grounds and sufficient larvae are produced to reverse the stock's decline. However, the potential of European eel stocks to recover is uncertain because the processes that determine how European stocks are sustained are not fully understood. In particular, the technical difficulties of studying the marine ecology of eels have hampered the development of knowledge about the critical phases of spawning, population structure, larval transport, recruitment and spawner escapement.

The EELIAD project was a four year EU-funded project (2008 to 2012) with the objective to improve the understanding of the marine ecology and biology of European eels. Field studies were undertaken to map and characterise the ocean migratory behaviour of eel. Over 500 electronic tags were attached or implanted to eels to record data as they migrated west to the putative spawning area. To date, more than 150 datasets have been retrieved that have mapped the migration more than 3000km and for periods of more than 6 months, and have yielded a database of behavioural data that is unequalled on any anguilllid species elsewhere in the world. Characteristic daily patterns of behaviour have been recorded that appear to be related to antipredator behaviour, thermal regulation and navigation. Predation was a significant cause of mortality of migrating silver eels, and occurred in both coastal and oceanic environments. Spawning ecology and effects on population structure were tested using genetic, otolith microchemistry, and modelling methods. Critically, the analyses were undertaken on eel larvae collected in the Sargasso Sea as well as on glass eels collected from the coastline of Europe and north Africa.

The results reaffirmed that eels are a rare but classical example of a panmictic species. On this basis, modelling of larval drift from the Sargasso Sea showed that climatic and oceanographic changes over the last 50 years do not appear to be responsible for the sharp decline in eel recruitment observed over the last 30 years, but was unable to resolve ongoing uncertainty regarding the duration of the larval migration. The influence of estuarine factors affecting glass eel runs was investigated using a hydroclimatic modelling approach. The model was validated using tidal and light data, and subsequently used to assess glass eel fisheries scenarios. A large-scale sampling programme was undertaken to collect comprehensive data on the health and quality of eels, resulting in the creation of a new EU silver eel quality database. Assessment of the data show that there are regional differences in parasite load, contaminant levels, fat content and breeding potential of silver eels that are related to catchment characteristics and biogeography. At the catchment level, regional differences occur in stock status, spawner escapement and anthropogenic mortality. Modelling of catchment characteristics and these parameters provided new tools that have the potential for operationalisation within national eel management plans.

Considerable efforts were undertaken to integrate with stakeholders and disseminate information about the need for improved management of eel stocks, the purpose of the project and the results that have emerged from it. At present, 19 papers resulting from the project have been published, with a predicted total of more than 50 within six years of project commencement. More than 50 presentations were given at national or international scientific conferences, and more than 20 workshops or discussion forums have been attended to contribute to discussions on eel biology and management. The work in the EELIAD project has been communicated to ICES and recommendations arising from EELIAD work are presented in this report. The project has featured on national and international television, in national and international press, and online. The work conducted within the project can genuinely be said to have reached an international audience numbering in the millions. In total, the activities conducted within the EELIAD project have resulted in significant advancement of knowledge, the development of advice and tools that will contribute to sustainable eel management, and global dissemination of project results that enhance the reputation of European-funded science.

Project Context and Objectives:

The stock of the European eel (Anguilla anguilla), like those of the Japanese and American eel, has declined dramatically in recent times. The stock is now judged to be outside safe biological limits and requires a Recovery Plan. However, the potential of European eel stocks to recover is uncertain because the processes that determine how European stocks are sustained are not fully understood. However, the potential of European eel stocks to recover is uncertain because the processes that determine how European stocks are sustained are not fully understood. In particular, the technical difficulties of studying the marine ecology of eels have hampered the development of knowledge about the critical phases of spawning, population structure, larval transport, recruitment and spawner escapement.

To this end, the EELIAD project was designed to address some of these questions. The overall goal of the project was to develop an integrated understanding of the behaviour and ecology of European eels in the marine environment to provide relevant and useful information for the European eel management plan. This required that the migrations of a representative sample of silver eels was mapped and characterised, that the ecological and biological features of migrating eels was determined, that a better understanding of the link between the adult stock size, migratory potential, the marine environment and juvenile recruitment was developed, that the genetic structure of the European eel population became better understood and that the knowledge developed was disseminated to stakeholders to inform and assist in the development and implementation of eel management plans. The EELIAD project was organised into seven workpackages, covering a total of 21 deliverables and 12 milestones, spread over an original implementation period of four years. The project started in April 2008 and was extended in 2011 to four and a half years with permission of the European Commission.

 The project was designed to take advantage of significant recent improvements in sophisticated scientific methods such as satellite telemetry, population genetics, molecular diagnostics, otolith microchemistry and advanced numerical modelling. These techniques were applied, often in combination, to the four main uncertainties of the marine life of eels, namely: the spawning migration, the origin and early life history of eels, the inshore migration of glass eels, and the quality and quantity of escaping spawners. For each of these uncertainties, several objectives were identified. Key to success was to ensure that the project was communicated to as diverse and wide an audience as possible.

Mapping spawning migrations

To achieve the goal of determination of spawning migration routes of female silver eels at the basin and -ocean-scale, it was necessary to:
1. develop new types of tag for recording the oceanic behaviour of eels
2. develop new techniques for tag attachment or implantation
3. undertake a large, Europe-wide eel tagging programme
4. Analyse recovered data to determine the migratory behaviour of eels, including route and habitat selection
5. Determine the factors that influence migratory success

Origin and early life history of eels

To achieve the goal of determining population structure and develop greater understanding of the larval migration, it was necessary to:
1. Undertake genetic analysis of larval eels collected in the Sargasso Sea
2. Compare genotypes of larval eels and successful migrants (glass eels) collected from across Europe
3. Assess temporal genetic differentiation of eels collected across Europe
4. Develop and use otolith microchemistry methods to determine the length of the larval phase
5. Assess the climatic factors affecting larval migration success

Inshore migration of glass eels

To achieve the goal of determining factors that affect the inshore migration, it was necessary to:
1. Parameterise and validate a mathematical model of glass eel migration into an estuary
2. Use the validated model to test glass eel fisheries scenarios, and develop understanding of the factors affecting them
3. Develop and enhance the model so it can be adapted for any estuary

Assessing the quality of escaping spawners

To achieve the goal of determining factors that affect the quality and quantity of silver eels escaping from a catchment it was necessary to:
1. Develop terminal and non-invasive methods for assessing the physical, physiological, disease and parasite status of silver eels
2. Undertake a Europe-wide sampling programme to build a silver eel quality database
3. Assess the relationship between individual traits and eel quality
4. Assess the parasite, contaminant and disease load of European eels
5. Analyse and model the relationship between habitat occupation and eel quality
6. Estimate silver eel escapement from a number of catchments, in relation to river typology and anthropogenic hazards such as fishing and hydropower
7. Develop models to help forecast escapement and population structure, and to identify their use in the eel management plans

Engaging and communicating with stakeholders

The scale and ambition of the project required that as much effort as possible was invested in communicating the results to a wide range of stakeholders. Members of the EELIAD project team aimed to disseminate information on the project to a diverse range of stakeholders, including fishermen, fishery and catchment managers, policy makers, scientists and the general public. This outreach was to be achieved through a range of methods, as follows:
1. A public website and blog
2. Working directly with fishermen and catchment managers during the tagging and sampling programmes
3. Attendance and presentations to workshops with primary stakeholders
4. Attendance and presentations at scientific conferences
5. Publication of scientific papers and books
6. Representation on ICES and relevant international management and advisory groups
7. Articles in the popular press and online

8. Working with film-makers and television
9. Direct one to one contact through a project email address and through ad-hoc queries

Finding out more about the EELIAD project

One of the aims of EELIAD was to promote the knowledge we gain and to use it to good effect to help conserve eel populations in Europe. To assist with this, the EELIAD project is documented through a public website: http://www.eeliad.com, supplemented by a project blog: http://www.eeliad.com/Wordpress, where you can find out all the latest news. As the project comes to a close, the website will be updated and access to project publications will be opened up to the public, as well as reports from workshops and conferences.

Project Results:

Introduction
The European eel (Anguilla anguilla) has a remarkable catadromous lifecycle: mature adult eels spawn in the sea from which the resulting larvae migrate to the rivers of Europe, grow to partial maturity in freshwater for a period of 5 to 15 years, then return once again to the marine environment to make their second long-distance migration to spawning grounds, where they die after reproduction. Thus, whilst most of the eel population's production occurs in freshwater, its key life history events associated with reproduction and recruitment take place in the marine phase. Despite more than a century of research, much of the ecology, life history and biology of European eel remains a mystery because traditional large-scale ship-based research has not proved a reliable or cost-effective technique.

Eels play an important socioeconomic and ecological role in many European countries. The stock of the European eel (Anguilla anguilla), like those of the Japanese and American eel, has declined dramatically in recent times. Recruitment of glass eels has fallen to below 5% of peak levels (measured from the 1970s onwards) and catches of yellow and silver eels have declined from 40,000t in the the 1960s to less than 20,000t today. The stock is judged to be outside safe biological limits and an EU Eel Recovery Plan has been instigated to maximize silver eel production and escapement to the sea to maintain and increase the stock's reproductive potential. The corner stone of this proposed Regulation is the development of national/regional Eel Management Plans by Member States. These Eel Management Plans must include the means to manage the local eel stock against sustainability targets set at the European level, and means to monitor and verify the attainment of that objective.

The use of population modelling tools is crucial to the EU-ERP, but at present, eel population models only take into account the production processes thatoperate in the freshwater or estuarine environment, and even then at a relatively crude level. Thus, the potential of European eel stocks to recover is uncertain because the processes that determine how European stocks are sustained are not fully understood. However, the potential of European eel stocks to recover is uncertain because the processes that determine how European stocks are sustained are not fully understood. In particular, the technical difficulties of studying the marine ecology of eels have hampered the development of knowledge about the critical phases of spawning, population structure, larval transport, recruitment and spawner escapement.

The EELIAD project was designed to take advantage of significant recent improvements in sophisticated scientific methods such as satellite telemetry, population genetics, molecular diagnostics, otolith microchemistry and advanced numerical modelling.

These techniques were applied, often in combination, to the four main uncertainties of the marine life of eels, namely:
1. the spawning migration;
2. the origin and early life history of eels;
3. the inshore migration of glass eels;
4. the quality and quantity of escaping spawners.
The achievements within the EELIAD project around these four main aims are described in the following four sections.

1. Mapping spawning migrations

The spawning migration of the European eel from rivers and brackish waters in Europe to the Sargasso Sea (it is presumed) is one of the most impressive feats of animal migration and orientation, yet the behavioural mechanisms involved are unknown. Few silver eels have ever been caught in the open ocean, and the environments that eels are thought to use during migration are extremely difficult to sample with traditional equipment. However, studying the migrations and distribution of individuals or groups of fish at sea is technologically challenging and extremely expensive. However, the recent development of high-technological tools to study individuals and populations remotely using electronic tags now make it possible to significantly increase our knowledge of traditionally hard-to-study species at a much lower cost.

1.1 Developing methods to track eels across the Atlantic

Electronic tags can be used to obtain information on European eel migrations in freshwater and at sea. Optimal fish handling and tagging methods are required both to meet the ethical standards for use of animals in research, and to ensure that the tagged fish exhibit as natural behaviour as possible. There is a large body of literature on tagging effects in different fish species and life stages, especially on salmonids, but very few on eels. Unique morphological, physiological and behavioural features of eels necessitated evaluation and adjustment of handling and tagging methods. To overcome these challenges, laboratory and literature studies were performed to achieve a standard operation protocols for eel tagging.

This was achieved by conducting the following tasks:
a) collecting data on eel anatomy to gain information on limitations on tag size and placement;
b) determining new methods for anaesthesia of eels;
c) examining the effects of tag implantation and the use different suture materials for closing incisions when implanting transmitters in the coelom,
d) evaluating the potential for use of stomach implanted transmitters;
e) developing and testing attachment procedures for external pop-up satellite archival transmitters (PSAT).

1.1a Eel anatomy measurements for surgical implantation and intragastric insertion of tags

Thirty four silver eels of lengths between 380mm and 998mm were dissected to determine internal and external dimensions relevant to tagging. The length of the body cavity limits the length of transmitters that can be used for surgical implantation. Measurements of the body cavity revealed that a 100 mm long tag is suitable for surgical implantation in all eels greater than 380 mm body length, and that a 150 mm long tag was only be suitable for silver eels longer than 550 mm. Assessment of incision sites suggested that although it is advantageous to place the incision as close to the head as possible to reduce the ability of the eel to investigate and damage the surgical incision and sutures, moving the incision too close to the head increases the risk of cutting and damaging the liver. Distance from the snout to start of the liver constituted approximately 1/4 to 1/5 of the total body length of the fish, indicating how far from the snout the incision should be made to avoid cutting the liver. Assessment of internal organ dimensions and position showed that the length of the stomach limits the size of the tag that can be used. Length of stomachs of European silver eel varied between 47 mm and 185 mm, indicating that gastric tags should not be used in the smallest silver

eels, but that there was space for relatively long tags in larger eels. The distance from the snout to the start of the stomach constituted 15-23% of the total body length, indicating how far the transmitter should be pushed during the tagging procedure.

Outcome: Peer-review scientific report submitted to the journal of Animal Biotelemetry ('Recommendations on size and position of surgically and gastrically implanted electronic tags in European silver eel').

1.1b Determining new methods for anaesthesia of eels

Tagging fish often requires anaesthesia both to immobilise the fish and to minimise the stress responses and pain that the fish experiences. Eels can be difficult to anaesthetise using 'traditional' fish anaesthetics, so experiments were conducted to determine the efficacy of the two most promising anaesthetics, metomidate and Aqui-S vet (iso-eugenol), currently available. Their effect on the primary (plasma cortisol) and secondary (osmoregulation) stress responses were determined, as well as long-term survival.

Both anaesthetics were suitable in terms of time to enter anaesthesia (3.8 min for Aqui-S vet. and 2.6 min for metomidate) and time to recover. First movement was observed after mean 6.8 min (Aqui-S vet.) and 4.8 min (metomidate). Total recovery was obtained after mean 7.6 min (Aqui-S vet.) and 6.5 min (metomidate). Plasma cortisol increased during metomidate exposure and reached a peak during the recovery phase. No increase in plasma cortisol was detected during Aqui-S vet. exposure. The plasma cortisol in the metomidate exposed group was significantly higher than in the Aqui-S vet. exposed group during the anaesthesia and recovery phase. Hence, it appeared that metomidate was not able to block plasma cortisol, and instead may have been an additional stressor for the eel. However, there was no post-procedural mortality in any of the exposed groups during 4 months exposure to seawater, indicating that although Aqui-S vet. might be preferred, either anaesthetic would be suitable for use in field experiments.

Outcome: Peer-review scientific paper published in Aquaculture research ('The efficacy of Aqui-S vet. (iso-eugenol) and metomidate as anaesthetics in European eel (Anguilla anguilla L.), and their effects on animal welfare and primary and secondary stress responses')

1.1c The effects of tag implantation and the use different suture materials for closing incisions in eels

Intracoelomic implantation is the most commonly used tagging method for electronic tags in fish. We examined the long-term effects of surgically implanting a new design of data storage tag in European silver eel and compared the suitability of four different suture materials (braided permanent silk, permanent monofilament, absorbable material and absorbable antibacterial material). The tag consisted of an electronic unit and three floats mounted on a wire making the tag flexible and therefore able to follow the movement of swimming eels.

No mortality occurred during the 6 month study. The growth of tagged fish did not differ from the control group. The sutures were shed or dissolved slowly in all groups, with no clear advantage to absorbable sutures. Wound inflammation was lowest in fish with monofilament sutures, perhaps because braided materials of the other suture types

allowed water to penetrate through the suture material, with increased risk of infection. Antibacterial treatment in one of the groups with absorbable sutures had no detectable effect on inflammation reactions or healing rates. Over the long-term, the tags caused an internal tissue reaction, with fluid in the body cavity and discolouration of internal organs. After 6 months, the transmitter became visible through the incision in 12% of the tagged fish (n=5). The internal reaction was stronger around the floats than the electronic unit, suggesting that the silicon coating material of the floats created a tissue reaction, and was not a typical reaction to electronic tags in eel.

Outcome: Peer-review scientific paper accepted in Marine and Freshwater Research ('Evaluation of surgical implantation of electronic tags in European eel and effects of different suture materials')

1.1d evaluating the potential for use of stomach implanted transmitters

Intragastric insertion of tags involves pushing the tag via the mouth down the pharyx and into the stomach. This may be a quick and suitable tagging method in European silver eel, especially as they have ceased feeding at this life stage. However, due to the focus in the EELIAD project on external attachment and internal implantation, no studies on tagging effects were performed in European eel. More knowledge is needed on regurgitation rates and on the susceptibility of damaging the gut wall during tagging.

1.1e Attachment of pop-up tags

New and smaller pop-up tags have made it possible to tag and follow ocean migration of the European eel. For animal welfare and data quality, it is important that the external tag attachment influences the fish behaviour as little as possible and the tag remain in place as long as possible. response to being tagged, and 3) physical damages to the fish from the different attachment methods. Four different methods of external attachment were tested. One methods had previously been described, while three were new to the EELIAD project. All eels survived until they lost their tag, or until end of the study (6 months). Specific growth rate did not differ between tagged and control fish. However, post-attachment response and tag retention after 6 months varied between attachment methods.

A tagging method developed during the EELIAD-project (termed Westerberg method) that utilises the strength of the silver eel skin by attaching the tag to the skin in three attachment points, is recommended for future studies based on a long tag retention time, minimal behavioural reactions after tagging, no damage to the swimming muscle, and minimal physical damages to the fish both for fish retaining and those losing the tag. Furthermore, if observations of ocean migration is the target of the tagging experiment, we recommend the transport and release of tagged fish offshore where it is less likely that the fish will move to the seabed and potentially lose the tag due to tangling in structured habitats. Outcome: Peer-review scientific paper submitted to Animal Biotelemetry ('Development and testing of attachment methods for pop-up satellite archival transmitters in European eel')

1.2 Tracking silver eels in the ocean
Mapping the marine migrations of eels has been a research goal of the scientific community in Europe, America and Japan for several decades,

arguably dating back to the discovery that Anguillid eels spawn in the marine environment at distant locations to their freshwater growth habitat. Early attempts to track eels in the deep ocean (Mediterranean and Sargasso Seas) were undertaken using ultrasonic telemetry, but these experiments achieved only very short records of eel behaviour from only 12 individuals. None of these tracking trials produced significant advances in the knowledge of likely spawning areas, partly because it was not feasible to track a large number of eels and because tracking became increasingly difficult as eels travel further from the release site. Thus, very little is known about the behaviour of eels once they leave coastal waters and move into deeper, oceanic waters, for several reasons. Firstly, the migration routes of virtually all eel species are unknown, and as a consequence all attempts to capture eels in the ocean have failed. Secondly, the cost of oceanic fieldwork is very high, and this mitigates against large and frequent efforts to search for eels over large ocean expanses. Finally, the equipment to follow eels over huge distances has, until recently, not been available.

However, the advent of pop-up (satellite tracking) tags at the start of the 21st century offered the possibility of being able to track migrating eels at sea, as well as providing information on their swimming depths and speed. A major advantage of this technology is that, once the tagged eels have been released, information on their swimming behaviour and migration is relayed to a satellite when the attached tag pops up to the sea surface- there is no requirement for a vessel to follow the fish, or a fisherman to catch and return a tag.

To take advantage of this opportunity, a large-scale tagging programme was initiated with the following objectives:
a) Development of new types of archival tag to collect data on the migratory behaviour of eels;
b) Deployment of archival and pop-up satellite tags on a representative sample of European eels;
c) Recovery and databasing of data on the migratory routes and behaviour of European eels;

1.2a Development of new types of archival tag to collect data on the migratory behaviour of eels

Eel tracking experiments using pop-up satellite tags had been trialled successfully in the Danish Galathea experiment in 2006. The information collected from the tags provided impetus for the development of new forms of archival tag for implantation or attachment to eels. The criteria for these tags were simple: to be as small as possible, to incorporate flotation that would enable drift to shorelines and to reliably store information on the oceanic migration of eels for a period of several years. This kind of data recovery device had been trialled before, but not on a large scale. The concept quickly became known as the 'flotsam tag'. The archival tag chosen for use in the flotsam tag was the Cefas Technology Limited G5. This tag houses a depth sensor that is temperature compensated in the range 2-34oC. The pressure range chosen was 1 000 m with ± 10 m accuracy and 0.3 m resolution. Temperature accuracy was ±0.1°C and resolution 0.031°C. The response time to reach 66% of a step change in temperature is 28 sec for the unmodified tag exposed to moving water.

Two types of flotsam tag were designed from this base. The first was an implantable tag (hereafter termed the i-DST, which was fitted with a

string of 11mm diameter floats (the same diameter as the tag). The total length with the floats was approximately 140 mm, weight in air 9.8 g and the net buoyancy was 0.009 N, corresponding to a negative weight in water of 0.9 g. The second was an externally attached tag (hereafter e-DST), which combined a bespoke pop-off mechanism and the G5 tag in a cylindrical float with the diameter 20 mm and length 130 mm.

The weight of this tag in air was 34.5 g and the net buoyancy in water was 0.046 N. The floats of both i-DST and e-DST were from syntactic foam with a crushing limit of approximately 1500 m and were painted in bright orange to facilitate detection on the beach. For an implanted DST the response time to the environmental temperature is determined by the thermal response of the eel, which is unknown and probably differs if the eel is alive or dead. The e-DST is insulated by the float and the response time was approximately 2.5 minutes. The suitability of these tag types for data collection in European eels is detailed in section 1.1.

Outcome: Knowledge transfer, development of flotsam tag technology (taken up by researchers in the UK, Germany, Denmark, Ireland, and under consideration elsewhere)

1.2b Deployment of archival and pop-up satellite tags on a representative sample of European eels

The tagging programme offered the opportunity to learn an incredible amount about the oceanic phases of eel behaviour and life-history, but it was also the most risky part of the project. The philosophy of the tagging programme was to minimise the risks and maximise the chances of success, and this cut across all of the elements of the tagging programme, from identifying tagging locations, to determining how to store and access the resulting data. To achieve this aim, the EELIAD was designed to have a two-phase tagging programme using both satellite and flotsam tags. The first year of tagging was targeted at sites where we expected the greatest probability of success, and to provide an opportunity to learn lessons that could then be applied in successive years.

Overall, 641 eels were tagged and released in four EU states and 11 eels were released at the mid-point of the oceanic migration in a collaboration with Reinhold Hanel of the Johann Heinrich von Thünen-Institut, Federal Research Institute for Rural Areas, Forestry and Fisheries, who led an expedition to the Sargasso Sea in 2011. All eels tagged were female eels, chosen for their large size and weight. Assessment of their physical characteristics confirmed that the eels were in an advanced stage of maturity (Pankhurst index greater than 6.5), and that morphological changes were consistent with readiness for the oceanic migration (fin index greater than 4.5). Outcome: Database of tagged silver eels, their physical characteristics and release locations. Peer review paper submitted to Fisheries Research ('Reliability of nonlethal assessment methods of body composition and energetic status exemplified by eel (Anguilla anguilla) and carp (Cyprinus carpio)')

1.2c Recovery and databasing of data on the migratory routes and behaviour of European eels

To date, more than 170 datasets have been recovered from eels tagged between 2008 and 2011. The majority of datasets have been recovered from PSAT tags, totalling over 4000 days of data. I-DSTs have yielded the

greatest proportion of data (nearly 7000d of data), while e-DSTs have provided some of the highest quality data from the oceanic migration (1200d data). The pattern of recoveries of pop-off satellite tags shows a general convergence of eels on the Azores (i.e. the bearing of eels from northern Europe shows a steeper trajectory than those from southern Europe), and is consistent with a migratory route that picks up the eastward flow of the Azores current. It is unlikely that they will turn back south-east to follow the Canary current and then into the return flow of the subtropical gyre. The main migration direction is therefore against the current. The flotsam tags were predominantly recovered along the western coastal margin of Ireland, Scotland (including the western and Shetland Isles), with some recovered from the west coast of Norway.

Highlights of the tag recoveries include datasets from several eels that migrated over 2000km from their release positions, the discovery of stereotypical dive patterns that characterise the oceanic migration, the revelation of environmental experiences previously thought to be outside of the physiological tolerance of eels (rapid pressure changes, water temperatures less than 0C), and the uncovering of background levels of natural mortality that have previously been impossible to observe or estimate.

Together with the data collected during the Galathea III project, the database currently holds more than 12,000 days of data on eel behaviour, of which approximately 50% (6000d) describes the coastal and oceanic migration of eels that escaped to the sea, and 50% describes the over-wintering and lacustrine residence of eels that did not escape to the sea.

Outcome: Database of eel behaviour at sampling frequency between 10s and 30min, totalling greater than12,000d data. Peer review paper published in the Journal of Fish Biology ('The anguillid eel migration problem: 40 million years of evolution and two millennia of speculation') and chapter in the Online Encyclopedia of Fish Physiology ('Migration of eels')

1.3. Factors influencing the migratory behaviour of eels

Laboratory studies of eel swimming have shown that eels are physically capable of reaching their far-flung spawning areas, but they do not provide evidence that eels can achieve this feat under natural oceanic conditions, where counter-currents, navigational issues, predators and more await. The recovery of a large dataset from eels tagged at various locations across Europe provided the opportunity to describe the natural behaviour of silver eels in the marine environment, and to determine the factors that influence swimming behaviour, environmental experience and migration success.

The tagging programme had three main aims, as follows:

a) To describe the migratory routes and behaviour of eels;
b) To determine the factors that impinge upon migratory success;
c) To compare the performance of stocked and unstocked eels to gain insight into navigational mechanisms

1.3a. The migratory behaviour of eels

Migration trajectories calculated from PSAT tags attached to eels released from Ireland and France show rapid movement offshore and into

deeper water and a convergence of routes at a location close to the Azores. The migration routes of eels released from Sweden follow a clear 'Nordic' route, with the Norwegian Trench as a strong restriction on the migration route. After leaving the Norwegian Trench, the eels move into the Norwegian Sea and most turn southward to follow the Faroe-Shetland channel and across the Wyville-Thomson ridge. One in four of the eels pass north of the Faroe Islands and cross over the Iceland-Faroe ridge. No eel took the deepest passage between the Faroe Bank and the Faroe Islands. An ongoing analysis of the by-catch of silver eels in bottom trawl surveys in the North Sea and the Baltic also confirm that this is the main migration route of eels from the Baltic and Kattagat-Skagerrak area. The Nordic migration route appears to converge on the route taken by eels released from Ireland. The speed of migration of eels released across the tagging programme varied between 5 and 50km per day. Distance travelled by eels ranged from only a few km, to over 2500km. Observations of migratory behaviour ranged from less than one day to over 10 months. Although the ambition of tracking eels all the way to Sargasso Sea was not realised, the mapping of migration routes and the data collected represent the most successful efforts to track eel migrations to date, and provide new insights into eel migration.

During migration, eels adopted a stereotypical pattern of vertical migration. Eels moved daily from an average depth of 500m (at night) to 900m (day) and experienced temperatures ranging from -1°C to 19°C. However, these overall averages mask a pattern of increasing depth as eels migrated further offshore, with thermal experiences that mirrored the water column structure. Thus, as eels moved west and into deeper water in late spring, average depth and temperature were greater than earlier in the year at more easterly locations. The occupation of deep water appears to be a response to predator avoidance during the daytime, when predatory fish and whales are known to dive to the depths where the eels swam during daytime. While this would mean that eels occupy cooler water at night, with consequent effects on metabolic rate and swimming efficiency, this may be necessary to delay gonad development until later in the migration. The occupation of shallower water during night-time may be needed to increase metabolic rate and muscle efficiency, or to search the water column for directional cues for the overall migration. This is feasible because the vertical stratification in the ocean mirrors the horizontal water-mass distribution on a much compressed scale. This means that a fish can experience an ocean-wide variation of a property by exploring a few hundred meters in the vertical. This allows a fish to search out depth levels where the vertical variation of a particular property – say an odour – has its maximum, and where the gradient will be readily observable on the length scale of the fish. In this way the local, fine-scale vertical structure of the ocean could form the basis for orientation on even the largest horizontal scales. The data gathered by the tracking technology used in the EELIAD project is approaching this goal, but there is still a long way to go before we can finally decide between the possible orientation mechanisms. However, in light of the results we have collected a simple innate directional cue seems highly unlikely and a sequential imprinting of the route from the Sargasso to the continental growth area also seems to be ruled out. The nature of the migration – a true navigation using map and compass or orientation along some oceanographic feature – remains an open question.

Work in the EELIAD project has inspired and been integrated with the tagging of other eel species in including, Japan, Canada and the South Pacific Ocean. The most striking finding is that the vertical migration

pattern of European eels appears to be the same in all species tagged to date. This suggests that the vertical migration is a very important part of the oceanic behaviour and must serve some vital function.

Outcome: Peer review paper published in Science ('First empirical results on the ocean spawning migrations of the European eel (Anguilla anguilla)') in preparation for Proceedings of the Royal Society B ('Migration of European eels to the Sargasso Sea'), and to Marine Ecology Progress Series ('Migration behaviour of eels from the Baltic and Skagerrak region). Contribution has been made to a manuscript submitted to Marine Ecology Progress Series ('Oceanic migration behaviour of tropical Pacific eels')

1.3b The factors that impinge upon migratory success

One of the outstanding results of the tagging programme in the EELIAD project is the insight into the fate of eels on their oceanic migration. The releases of eels from Ireland, France, Sweden and Spain produced differing rates of migratory success, and the data return for some areas was poorer than expected. Many of the external PSAT or archival tags were released prematurely, many within 7 days of being released. The reason for the rapid loss of tags is not fully understood and while loss of the tag due to rejection or mechanical failure of the attachment cannot be excluded, a 6-month laboratory study of the attachment methods used in the project showed a high survival and retention. A more likely explanation is an unexpected high predation pressure on eels.

In more than 20 percent of cases, the fate of PSAT tagged eels could be confirmed as predation because the Microwave Telemetry X-tag stores for each day the highest and lowest measurements of daylight level. If the maximum light level was the same as the minimum even if the tag showed movements in the upper layer it can be concluded that the tag has been swallowed. In many of the other records there is a sudden switch from the regular diurnal diving cycle to a different pattern, e.g. a sudden drop to the bottom and the tag surfacing after 4-8 days. In a few cases the identity of the predator could be determined. Marine mammals were involved in at least four cases. This was concluded from the body temperature recorded while the tag was in the stomach. Another predator was a warm-bodied shark, which in this area could have been a porbeagle or a thresher shark. A high incidence of eel predation by porbeagle sharks have been seen for American eel in the Gulf of St. Laurence (Béguer et al., 2012).

Some eels did not escape to the sea, and instead overwintered. This behaviour was studied in detail in eels tagged with flotsam tags and released during autumn 2008 in Lake Mälaren in Sweden. Activity stopped typically at a temperature between 11 and 9 oC. Intermittent, short periods of swimming were seen down to an ambient temperature of 6C. From mid November to the middle of April (approximately 160 days) the eels lay motionless, buried in thebottom sediment. Activity started at a lower temperature than its cessation, in most cases between 3.5 and 4.5oC. The inactive period resulted in a significant loss of body weight, more than 0.4 g/day or a median loss of 6 % of the total body weight during this period. Migrating silver eels are able to swim actively at much lower temperatures than those triggering overwintering, so why do they go into torpor for a long period, loosing fitness and body fat? The eels tagged in this project were categorised as being migratory and in the silver eel stage. The reason why they nevertheless abandoned migration and went into

overwintering is unclear. It has been argued that stocked eels lose the ability to orientate correctly and the eels in Lake Mälaren are predominantly of stocked origin. If this were the case one would expect the eels to continue migrating randomly even at lower temperature. An alternative explanation is that the external characteristics that are used as indicators for silvering don't correlate with a true motivation to migrate. A fully developed migratory behaviour may therefore require cues from the marine environment.

After exclusion of eels that suffered predation, eels that appeared to become exhausted early on in the migration, or which did not escape from the freshwater environment, twenty five high quality datasets currently remain for detailed analysis. This number is expected to grow over time as more flotsam tags are recovered from coastlines. These datasets describe, in varying levels of detail, the daily and seasonal behaviours of ocean migrating eels, and comprise a database of over more than 2500 days, some 250 times as much data as has been collected over the previous four decades. The physical characteristics of these eels do not appear to be significantly different from eels that did not achieve a successful migration.

Outcomes: Contribution to peer review paper published in PLoSOne ('Shark Predation on Migrating Adult American Eels (Anguilla rostrata) in the Gulf of St. Lawrence'), chapter in the book 'Swimming physiology of fish' ('Extreme swimming: the oceanic migrations of anguillid eels'), chapter in the book 'Physiology and Ecology of Fish Migration' ('Migratory behaviour of the European eel') and three manuscripts in preparation (for PLoSOne, 'The tag, the eel and the whale'), (for Animal Biotelemetry, 'Fate of migrating European eels in the Atlantic Ocean'), (for the Journal of Fish Biology, 'Fitness by torpor in over-wintering European eels').

1.3c Comparative performance of stocked and unstocked eels

The dramatic decrease in recruitment of the European eel (Anguilla anguilla L.) during the last 30 years has motivated the European Union to introduce a regulation establishing measures for the recovery of the stock. The regulation lists a number of possible management measures that could be used in an eel management plan. The translocation of glass eels caught in recruitment rich catchments to recruitment poor catchments ('stocking') is one of those. Based on a series of tagging experiments in the Baltic, evidence suggests that translocated eels may not be able to migrate back to the Sargasso Sea successfully, with the underlying assumption that eels imprint the route from the Sargasso Sea to where they grow up, possibly by using a magnetic map or thermal and olfactory cues.

To examine the behaviour of eels in the freshwater environment, eels were equipped with acoustic ID-coded tags from the River Enningdal (natural recruits) and from River Ätran (stocked eels) were released in the innermost branch of Gullmarfjorden. All but one of the tags were detected at one or more of the receiver lines downstream. The period that the eels stayed in Gullmarfjorden varied. The first eel was registered at the mouth of the fjord 7 days and the latest 52 days after release. The time to escapement and swimming velocity showed no significant difference between stocked and unstocked groups (p=0.39). Offshore/ oceanic migration was studied using PSATs or flotsam tags. The salient results for the comparison between stocked and naturally

recruited eels are 17 tracks with duration between 1.5 and 5 months. Of those, 11 originate from River Ätran and 6 from River Enningdal. The total number of days with eel behavior data is 1227 for River Ätran and 606 for River Enningdal. All eels follow essentially the same route in Skagerrak and along the Norwegian west-coast. The main guide for the eels is the Norwegian Trench, where the depth is larger than approximately 200 m. In the Norwegian Sea the trajectories are more dispersed but except for one Enningdal eel the general picture is that the eels turn south-west and follow the continental shelf, past the Iceland-Scotland ridge into the Rockall channel west of Scotland. The range of the length and duration of the trajectories were 490-2450 km and 18-156 days respectively. The mean migration speed was 22 km/day with a standard deviation of 8 km/day. The ranges were approximately the same for both the groups of eels and there is no significant difference in average migration speed. All the eels showed a continuous diurnal depth cycle with a deeper swimming level during the daylight period and shallower during the night, which is typical of eels reaching oceanic depths. The daily amplitude varied both along the tracks and between individuals. There is no evident difference in diving behavior between the two groups.

On the basis of this experiment, it appears that there are no obvious behavioural differences between the translocated eels stocked as glass-eel in River Ätran and the naturally recruited eels from River Enningdal, nether in the initial behavior after release, nor in the subsequent offshore migration during several months. During the ocean phase of migration there is no statistically significant difference in the choice of route, depth preference, diurnal behavior or average migration speed. The initial delay and migration speed in the fjord experiment are the same. Although these results don't prove that translocated eels contribute to the spawning stock, the present results include the longest distances any eel, stocked or otherwise, has been tracked however, and cover approximately one third of the total distance to the spawning area.

Outcomes: Manuscript in preparation for the ICES Journal of Marine Science ('Behaviour of stocked and naturally recruited eels during migration').

2. Origin and early life history of eels

The larval life history is one of the less investigated aspects of eels life cycle due to the methodological difficulty in implementing surveys at sea (Schmidt, 1922). The question of the larval duration has been much debated as length frequency data can be interpreted to mean that some eels may remain as larvae for up to three years (Tesch, 1977, 2003; McCleave and Kleckner, 1987). This conclusion has been supported by a transport model (Ketel and Haines 2006). However, studies based on otolith microstructure SEM analysis showed that the larval migration is much shorter and probably lasts less than a year (Lecomte, 1991). Recent studies on tropical eels have shown that it is possible to use otolith analysis to retrace leptocephalus migration pathways, and duration of migration and therefore propose the location of spawning areas (Robinet et al., 2003).

Studies to sample eel larvae are expensive to perform and a logistic challenge to complete. Our approach was to use existing biological material to assess the larval stage, and to couple this with modelling exercises to test specific hypotheses about larval recruitment. This aspect of the project had three main aims, as follows:

a) Assessment of the population structure of the European eel stock
b) To estimate the duration of the larval migration;
c) To assess the origin and migration success of larval eels;
d) To investigate the potential impact of variation in oceanic currents
on the migration and recruitment of larval eels

2a Population structure of the European eel stock

The European eel has traditionally been considered an example of a
panmictic species, i.e. eels from the whole continental range of
distribution have been thought to constitute a single, randomly mating
population, which reproduces in the Sargasso Sea. However, a number of
recent studies employing molecular markers, in particular microsatellite
DNA, have challenged this view. One major problem with the studies of the
genetic population structure of European undertaken so far relates to the
sampling strategy. The eels studied are not caught on the spawning
grounds but at the European coast. Thus, any 'real' genetic structure may
have been blurred during the transport of larvae from the spawning areas.
We assessed the panmixia hypothesis using microsatellite DNA markers
applied to samples of leptocephali collected in the Sargasso Sea during
the Danish Galathea expedition (271 A. anguilla and 117 A. rostrata), and
on 21 samples of glass eels (a total of 1010 individuals representing 14
localities from Iceland to Morocco and including 9 samples taken from the
same localities but in different years or at different times within the
same years). All samples were genotyped a 21 microsatellite loci, and
species identification has furthermore been independently verified by
analyzing species-specific mitochondrial DNA cytochrome b markers. This
is the first molecular population genetics study based on the larvae of
both Atlantic eel species sampled directly at the spawning grounds,
supplemented by analysis of European glass eel samples. The analysis
provided strong evidence for panmixia in both the Sargasso Sea and across
all continental samples after accounting for the presence of sibs among
newly hatched larvae. So despite the fact that several recent studies
(based on continental samples) have found subtle, but significant,
genetic differentiation, we suggests that the European eel should still
be considered as a classical (but rare) example of panmixia. European
eel has declined catastrophically, and these findings call for management
of the species as a single unit, necessitating coordinated international
conservation efforts.

We also tested for "continental" genetic heterogeneity among maturing
adult eels and estimated the temporal genetic differentiation and
effective population size of the European eel stocl using microsatellite
DNA markers in silver eels whose age had been determined. The combination
of microsatellites with demographic information allows for the assessment
of temporal genetic differentiation and estimation of effective
population size per generation (Ne) and the effective number of breeders
per year (Nb), using complementary statistical methods. Genetic data for
six microsatellite markers were used for comparing maturing silver eels
of known age sampled in 2003 from southern and northern Europe. The
results supported the panmixia hypothesis; despite large sample sizes
there were no signs of genetic differentiation, and a power analysis
showed that the true level of spatial heterogeneity (if existing) must be
exceedingly small to have remained undetected. Since the original
analysis, the dataset has been expanded to include significantly more
individuals and gene markers. The aim of the current analysis is to
estimate the genetically effective size of the seemingly panmictic
European eel population. A data base comprising about 2050 silver eels of

known age, sex and body size, genotyped at 22 microsatellite markers from the "positive list" of loci, has been produced. The data base also includes genotypes for c. 50 specimens of A. rostrata genotyped at the same set of loci, to be used for comparisons and identification of putative species hybrids. There remains some ongoing statistical analysis to complete.

Outcomes: Peer review paper published in Molecular Ecology ('All roads lead to home: Panmixia of European eel in the Sargasso Sea'), peer review paper published in Heredity ('Panmixia in European eel revisited: no genetic difference between maturing adults from southern and northern Europe') and a manuscript in preparation Proceedings of the Royal SocietyB ('Stable but low annual effective population size in the declining European eel stock').

2b Assessment of the duration of the larval migration

About 2300 years after Aristotle, Lecomte-Finiger began her 1994 letter to Nature with "the early life history of the European eel Anguilla anguilla is still something of a mystery". Twenty years later, this assessment is still arguably true. Controversy still exists about the duration of the larval phase because otolith microstructural analyses suggest that the generally accepted 2-3 years duration suggested by Schmidt in 1922 could be revised downwards to less than one year. We used the otoliths from glass eels collected simultaneously in 9 different localities and over two consecutive recruitment seasons in 2 localities to further resolve this issue. The early-life histories of 385 European Anguilla anguilla glass eels were determined, and showed that larval duration variation was relatively low along the Atlantic coast but showed a clear gradient from western to eastern Mediterranean Sea. This suggests a frontal arrival on the European coasts and the existence of one large or different latitudinal routes of dispersal. Metamorphosis from larva to glass eel was correlated with the arrival at the continental shelf but the relationship between the onset of metamorphosis and metabolic rate suggested that there was also an endogenous 'clock' that determined the onset of metamorphosis. The biometric characteristics (total length, weight and condition) were examined for 900 glass eels collected at recruitment. Spatial variations seemed to corroborate the conclusions of the otolith analysis.

The transatlantic journey of A. anguilla larvae was estimated to last between 7 to 14 months. These durations are coherent with distances crossed (about 6000 km) compared to A. japonica (2600 km in 5 months to Taiwan, 3800 km in 7 months to Japan). Furthermore, the hatching period and the glass eels detrainment period along shelves corresponding to these durations extended from December to July and from October to January respectively, which is coherent with periods reported in the literature, but differs from estimates produced from passive drift models of dispersion. We therefore hypothesis that A. anguilla leptocephali may not be driven passively by oceanic currents but could at least orientate their body in the current. Further analysis is required to determine if incorporating more physical and behavioural (diel vertical migration) into drift models will support or refute the results from otolith studies.

Outcomes: Manuscript in preparation for the Journal of Fish Biology ('Variability of early-life histories of the European eel Anguilla anguilla').

2c assessment of the origin and migration success of larval eels

Whether the spawning area of European eels is located in a single site or at distinct sites is still unknown. The European eel spawning area, partly shared with the American eel, appears much more diffuse than the very localised spawning area of the Japanese eel. However, because no adult eels have ever been captured in the Sargasso Sea, a great deal of uncertainty remains regarding this topic. We compared the elemental signatures of otolith's core region of Anguilla anguilla leptocephali caught in the Sargasso Sea in 2007 with those of glass eels and elvers sampled in European estuaries during 2006, 2008 and 2009. Using laser ablation inductively coupled plasma mass spectrometry, the same annular ablation trajectory along the first feeding mark was applied on otoliths of glass eels, elvers and leptocephali.

A total of 13 isotopes representing ten elements were found in detectable concentrations in glass eels, elvers and leptocephali otoliths using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS). A total of 307 glass eels and elvers collected from 11 sites in 2006, 2008, 2009 and 16 leptocephali from the Sargasso Sea (2007) were examined for these elements at their otolith first feeding mark. The isotopes presenting the highest ratios were $86Sr$, $24Mg$ and $25Mg$. The concentrations of the thirteen isotopes in the otoliths of glass eels / elvers did not vary among three annual cohorts collected in eleven European locations. However, canonical discriminant analysis, based on concentrations of 11 isotopes, showed that the leptocephali samples separated clearly from all glass eel / elver samples along the first canonical variate. The same results were obtained using a cluster analysis based on Euclidean distances and a farthest-neighbour paradigm. Although the mechanisms that regulate the differences in trace element signatures among leptocephali and glass eels / elvers are unknown, we propose that the sampled glass eels / elvers were born in a spawning site or region where favourable transport and / or feeding conditions occurred. Conversely, the leptocephali may have been sampled in a less favourable region in the Sargasso Sea, with a low probability of reaching continental growth areas.

Although the exact location of the spawning site(s) remains unknown, the results of this study provide encouraging indications that elemental fingerprints of the otolith core region have potential for discriminating among A. anguilla spawning areas. Considering these facts, it seems to be reasonable at the moment, to suppose that several spawning areas for the European eel may exist. As long as the question has not been answered why the Sargasso Sea is so unique for Atlantic eels' reproduction, and as long as the exact location has not been confirmed, the entire area could be seen as potential breeding sites. Without additional studies combining genetic and otolith fingerprints and tracking migrating adults, we can only speculate from the present study on the geographic interpretations of European eel otolith microchemical signatures. However, the results suggest such studies may help clarify aspects of the spatio-temporal dynamics and relative levels of success of larval and silver eel migrations and spawning. These could be of benefit in informing management and conservation of the European eel in the light of the declines in recruitment seen in recent decades.

Outcomes: Peer review paper published in Ecology of Freshwater Fish('An otolith study of possible relationships between the origin of

leptocephali of European eels in the Sargasso Sea and the continental destinations and relative migration success of glass eels').

2d. The potential impact of variation in oceanic currents on the migration and recruitment of larval eels

Recruitment of the European eel is at a historic low level and continues to decline. All glass eel recruitment series show clear and marked reductions since the early 1980s. Over the last 5 years glass eel recruitment has averaged between 1% (in the continental North Sea area) and 7% (in the continental Atlantic area) of the 1960-1979 levels. A parallel decline in recruitment of the North American eel, with overlapping spawning area, lead to the hypothesis that there is a common ocean environmental factor causing decline. A simple Lagrangian model was constructed to simulate the passive drift of the European eel (Anguilla anguilla) leptocephalus larvae from the spawning area in the Sargasso Sea (50-70°W and 23-30°N) to the European shelf, and test this hypothesis. The simulation utilised the velocity data from a reanalysis of ocean climate, the Simple Ocean Data Assimilation (SODA 2.1.6). The velocity fields are available for every 5 days for the period 1958 to 2008 on a half degree horizontal grid and at 40 depth levels. The average drift time and latitudinal distribution of the arrival of eel larvae was then explored for a range of constant depth levels and instantaneous mortalities. The period which was modelled covers the time of the regime shift in eel recruitment.

The average time of the passive cross-Atlantic drift was about 20-24 months, with a minimum transportation time of eleven months. Due to high velocities of the Gulf Stream this path was often dominated by faster drifters, crossing over in less than 18 months. The success and survival due to passive drift give no support for the hypothesis that a climate shift in the circulation of the subtropical gyre is the reason for the decline in recruitment of glass eel in Europe. On the contrary, given a constant output from the spawning area the recruitment should have been at an all-time high from 1995 to 2004. Over a shorter time scale there is a certain tendency for the peaks in drift success to coincide with peaks in glass eel recruitment 2 years later. This lag is to be expected if the larval drift time is 20-24 months. Given that the ocean model data are realistic there are several possibilities to use this kind of simulation to address other questions. The model can be run backwards in time to explore the area of origin of larvae arriving in a particular place. One such question is where the mixed population in Iceland originates in the overlapping breeding places of A anguilla and A rostrata. Another long-standing question is the difference in travel time between what is seen in counts of daily otolith rings and the estimates from passive drift. The age according to the otolith count varies for different part of the eel range and a comparison of the drift time between places with known otolith ages and a back-calculation to possible spawning places could help in clearing up the discrepancy between the methods and give limits for the necessary directional active swimming component needed.

Outcomes: Peer review paper in press in Ecology of Freshwater Fish ('Climate change and passive transport of European eel larvae').

3. Inshore migration of glass eels

Following their migration from the spawning site(s) to the European coast, larval eels metamorphose into glass eels before entering rivers (Tesch, 2003). Many studies have been made on the migratory behavior of the glass eel in estuaries. Typically, glass eels only rise above the substrate when the tide flows upstream, and remain close to, or buried in, the substrate when the tide is downstream. Factors affecting the level of success of up-river survival of glass eels have significant effects upon eel population structure e.g. density and sex ratio, and consequently upon the quality and number of silver eels that eventually escape and migrate. Furthering our understanding of the different factors that affect the survival and settlement of glass eels was a relatively small part of the EELIAD project that was progressed through the use of mathematical and statistical models of glass eel behaviour, with the aim of improving our existing understanding of glass eel migration in a case study estuary, the Adour, before developing this model for application in different estuaries and situations. A secondary aim was to use the model to estimate and test fisheries management scenarios.

Studies were carried out on the Adour estuary on the migration of glass eels lead to the characterisation of their swimming behavior. Individuals migrate passively with the flood tide current behind the dynamic tide front, and their movements into the water column are linked to the surrounding luminosity and water turbidity. A numerical model was built from observations gathered on glass eel densities during scientific surveys. It uses the outputs of a hydrodynamic model accounting for the variations in the river flow and tide coefficient. It allows the simulation of the displacement of a particle in the longitudinal axis of the estuary. The variation of the vertical movements through the water column takes into account the cloud cover, the moon phases, the alternation of days and nights and the water turbidity. Additional data in relation to glass eel sensitivity to the illumination were incorporated and have enabled quantitative analysis of glass eel vertical position in the water column of an estuary as a function of light level.

The results allow displaying the migration speed of groups of glass eels entering the Adour estuary. These simulations are validated by the comparison with in situ observations and the outputs of the behavioral model make possible, on the one hand, to simulate the migration speed of glass eels according to hydrological data and, on the other hand, to define the environmental conditions that stop or slow down their displacement into the estuary. The simulation of migration provides estimates of the average migration speed in relation to hydroclimatic conditions and can help determine how many runs of glass eels are available to the pushed scoop-net fishery during a given flood tide in certain areas of the estuary.

From these estimates and reported catches made by the fishery during the same night, the exploitation rate applied by the fishery on the flow of glass eels progressing upstream during night flood tides is estimated. The relationship between the exploitation rate, fishery catches and hydrodynamic conditions allowed the estimation of the exploitation rate and nocturnal biomass fluctuations during the fishing season, from November 1st to March 31st of the following year. Finally, from the chronological series of biomass migrating at night, the total biomass migrating every day and the total recruitment into the estuary, during the main glass eel migration period, are estimated. Estimations made between 1998 and 2005 indicate that the overall rate of exploitation of

the marine and continental fisheries, on average, is of 15.7%, ranging
between 8 and 25% according to fishing seasons.

Further spatial and temporal refinements have now been incorporated and
tested, resulting in a successful validation/ proof of the model. In
consequence, the model has been successfully adapted to enable its
application to other tidal estuaries, and is now available on line at
https://redmine.univ-pau.fr/projects/glasseel2d. This application has
been designed to allow end users to simulate glass eel migration in tidal
estuaries, and to provide a range of outputs that can be used to assess
the catchability of the glass eel run according to the hydroclimatic
conditions observed a given day and a given fishing season (rate of flow,
tide level, turbidity, moon phases).

Outcomes: Peer review papers published in Aquatic Living Resources
('Daily and seasonal estimates of the recruitment and biomass of glass
eels runs (Anguilla anguilla) and exploitation rates in the Adour open
estuary (Southwestern France)', and 'Analysis and visualization of the
glass eel behavior (Anguilla anguilla) in estuary and estimate of its
upstream migration speed'),peer review paper published in Mathematical
Modelling of Natural Phenomena ('Modelling and Mathematical Analysis of
the Glass Eel Migration in the Adour River Estuary'), peer review paper
in press in the Journal of Hyperbolic Differential Equations ('The Cauchy
problem for a conservation law with a multiplicative stochastic
perturbation'), online publication of glass eel modelling tool
('glasseel2d')

4. Eel quality and escapement

Environmental factors have an influence on the 'quality' of individual
eels that may affect their ability to migrate to their spawning grounds.
Previous studies have estimated that eels theoretically require a total
body lipid concentration exceeding 15-20% for successful oceanic
migration, gonad development and spawning However, it has yet to be
established whether lipid content, or other aspects of body condition,
affect life history 'choices' earlier in the yellow eel stage. For
example, recent laboratory experiments suggest that levels of pollutants
(PCBs) and the occurrence of infection by the EVEX virus or Anguillicola
parasite may have a significant effect upon migratory ability of silver
eels, leading to a diminished reproductive potential within the European
stock as a whole, and contributing to considerable variability in
migratory potential between rivers. However, existing models cannot take
into account the effects of varying quality of silver eels because large-
scale surveys of silver eel quality have never been carried out, and the
characteristics of rivers that lead to variation in eel quality have not
been established.

4.1. Development of methods

Defining the 'quality' of silver eels is not a straightforward process,
since the characters that identify eels as high or low quality have not
yet been identified. Simple measures, such as percentage fat content or
total contaminant load, are currently being debated or used as indicators
of eel quality. However, such measures provide a very limited indicator
of the quality of eels escaping a catchment because the contribution of a
catchment to the spawning stock of eels depends on both the quality of
eels as well as their quantity. Thus, while small catchments tend to
generate smaller silver eels, the numbers of escaping eels are much

higher compared to large catchments. Thus, the overall contribution may be the same or greater. Secondly, assessments of lipid content alone do not provide a full picture of breeding potential because other physiological and physical characteristics also need to be taken into account, such as pollutant load and parasite/ disease infestations.

We identified the need to:
a) Undertake a comprehensive assessment of the characteristics that are or may be related to the quality of silver eels in Europe;
b) To develop non-invasive molecular methods to test for pollutants and diseases that are considered to have an important bearing on the spawning success of eels;
c) Development of methods to improve the value of life-history information extracted from otoliths.

4.1a A comprehensive assessment of the characteristics relating to silver eel quality

A detailed protocol for trapping and sampling silver eels across a wide geographic range was developed to provide a comprehensive assessment of silver eel quality. The protocol focussed on the collection of data and tissues to enable analyses of morphometric, physiological and health characteristics. Silver eels were sampled in the autumn of 2009 at ten sites. The sampling effort, which was quite unprecedented, was made possible by the integration of effort across seven partners, led by MNHN, who each received a dissection kit specially prepared for the assessment. Special attention was paid to labelling to ensure the results could be tracked accurately and to meet quality assurance guidelines. A total of 446 silver eels were sampled, measured, dissected and stored. Each eel was processed according to the detailed protocol that included measures of size, tissue samples (blood, organs and muscle), and otolith extraction. Data and tissue samples were compiled and processed by the MNHN with the collaboration of the University of La Rochelle. A variety of analyses have been undertaken on physical, physiological and chemical aspects of eel quality, as detailed in section 4.2.

4.1b The development of non-invasive molecular methods to test for pollutants and diseases

A general approach was developed to assess the effect of contaminant loads and parasite contamination on the expression of CYP1A1 and MXR candidate genes on eels sampled in the Adour estuary. Tools were developed to identify the interference of pollutant loads on productivity, escapement and migratory success. The work enabled the development of a reliable methodology to detect variations of gene expression using RTPCR methods. However, no significant variations of gene expression were detected according to exposure to contamination (metals and PCB). However, an otolith microchemistry approach was developed that could be used to assess habitat occupation, and therefore infer the potential exposure to toxins in different environments.

A specific, sensitive and reliable genotyping tool able to detect, identify and quantify different strains of EVEX and EVA viruses was developed using infected eel tissues from internal organs. This tool was validated using both positive and negative samples, and is presently under a patent pending. The molecular tool was used to detect possible infections in silver eels collected in 2009. None of the 50 silver eels analysed was infected by EVEX. Since this test requires the dissection

of eels, two non-invasive methods (a direct tool, using genotyping, and an indirect tool, using ELISA methods) have been under development. To date, this task has proven frustratingly difficult to complete because infected eels are difficult to source, and experimentally infected eels do not always express the virus. This particular task is extremely challenging. We highlight that, to date, no group has been able to diagnose directly the presence of a fish rhabdovirus by a non-invasive method.

4.1c Development of methods to improve the value of life-history information extracted from otoliths.

Because the entire lifetime of the fish is virtually recorded in the otoliths, a large amount of information can be interpreted using them. This information includes age and growth, and the latest sophisticated chemical techniques allow the reconstruction of many traits from the year of hatch, migration pathways, to the temperature of the water, etc. However, methods used to extract information are often exclusive (a treatment needed for age estimation generally precludes later microchemistry analysis), and it is generally not possible to spare one "raw" otolith for potential new investigations and/or archival purposes. In this context, we developed a conservative approach (no chemical treatment as etching or coloration) that aimed to use only one otolith for both age determination and microchemistry analysis (ICPMS). To achieve this, about 200 otoliths were prepared and aged using a standard method of encapsulation and polishing, and compared to other methods where otolith preservation is not possible. Although the new method can be time-consuming, the results revealed that this standardised method presents many advantages particularly when large-scale sampling programs are involved.

Outcomes: Peer review paper in preparation for the Journal of Fish Biology ('How to age eels without excluding other analyses'), patent pending on a molecular tool for detecting EVEX and EVA virus, first comprehensive database of European eel quality parameters.

4.2 Assessment of eel quality

The combined dataset of life history traits, heavy metals and POP loads, parasite communities (450 silver eels sampled during their downstream migration across European inland habitats) has now been databased. This database is a significant project asset now available to the project consortium and future collaborators.

The database contains information on key parameters, and is being used to investigate the interrelating factors that contribute to eel quailty:
a) Individual traits of eels
b) Parasite load
c) Pollutant and contaminant load

4.2a Individual traits and eel quality

Data collected on the individual traits of silver European eels sampled across the species geographic range are being combined to assess the reproductive 'quality' of the eels -an expression of their ability to migrate, to breed successfully and to produce a viable offspring - in relation to ecological and geographic clines, eg latitude and longitude, together with local environmental characteristics such as salinity and

catchment size. The generally recognised hypothesis is that there is (i) a positive and significant relation between age at silvering and latitude and (ii) that size increases with latitude. Our results confirmed that age is correlated to latitude but that the best fit was found with minimum age rather than with maximum age and average age. This suggests that the duration of the growth stage may be controlled by parameters linked to latitude (ie temperature, light) together with local conditions (salinity, food resources) and/or phenotypic characters. The weight of silver males and females was not related to latitude, but there was a significant relationship between weight of females and size of the catchment. This could be due to lower intraspecific competition for space and food in large river systems than in small ones. This interpretation is supported by an assessment of the length of eels and in relation to latitude and river type, which shows that rate but is modulated by the nutrient and salinity of the catchment. Statistical modelling of the dataset is ongoing.

4.2b The relationship between eel quality, parasites and disease

Parasitism is one of the reasons evoked to explain the collapse of the European eel, in particular those exerted by introduced species, i.e., the monogenean Pseudodactylogyrus sp. in the gills and the nematode Anguillicoloides crassus in the swim-bladder. We have studied metazoan parasites of 149 silver eels originated from 5 sites in northern Europe. In total, 88.59% of the eels were infected by 14 species of parasite. A. crassus was dominant (56.03%), followed by Acanthocephala (38.93%) and Pseudodactylogyrus sp. (17.29%). Data analysis show inter-site differences in the composition of parasite communities, with consequences in terms of direct impact at host individual (pathology) and population (fitness) scales. Silver eels from the Swedish site Malaren are the less parasitized with a total prevalence of 40% (vs 90-95% for other sites), and by the total absence of parasites in their gills. The Irish site Burrishoole (pristine site) greatly differs from the others by the total absence of A. crassus and by the high prevalence (85.71%) and occurrence of intestinal acanthocephalans (intensity = 29.88 ± 4.34, abundance = 25.78 ± 2.36). Even if less pathogenic than Pseudodactylogyrus sp. and A. crassus, when in great number in the intestine acanthocephalans can significantly injure the intestinal wall of their host and compete for nutrients, in particular lipids. Lipid depletion induced by acanthocephalans can thus compromise the transoceanic spawning migration. Further research needs to focus on interactions between hosts, parasites and pollutants both in controlled conditions and in the field. In particular, from the many parasites identified in A. anguilla, acanthocephalans have to be the object of future detailed investigations. One question is whether to harbor these helminthes in the intestine could be advantageous for A. anguilla since they represent a potential detoxification pathway in case of heavy metal exposure or if they are also detrimental to the host because they induce a lipid depletion that can compromise the successful completion of the spawning migration.

We examined the biological responses of eels to infestation by parasite communities, and more specifically to the invasive nematode Anguillicolloides crassus. A total of 484 silver eels were examined for epidemiologic parameters and SDI (swim bladder degenerative index). In most of the investigated catchments (8 of 12) more than 70% of the eels were infested with A. crassus, the highest percentages of infection being recorded in France (Frémur: 94%, Loire: 92%), Denmark (92%), UK and Belgium (89%). The lowest percentage of infection was found in the

Swedish site Malaren (54%), the Spanish Rio Esva estuary (38%), the
French Mediterranean lagoon Bages-Sigean (8%) and finally the Irish
Burrishoole River (0%). A swimbladder damage index was measured for eels
in each catchment, showing that, with the exception of France Bages-
Sigean, Spain Rio Esva and Ireland Burrishoole, 17% to 60% of the silver
eels displayed a SDI = 4 and consequently may not have been able to reach
the Sargasso Sea. Eels from UK catchments had the most damaged swim
bladders (highest % of silver eels with SDI=4). However, even for
preserved sites such as France Bages-Sigean, Spain Rio Esva and Ireland
Burrishoole, a non negligible proportion of the eels had damaged
swimbladders. There was a significant positive correlation between SDIs
and total number of A. crassus. We also found a negative significant
correlation between Le Cren condition factor of female silver eels and
total number of A. crassus. In addition, female silver eels whose total
number of A. crassus is greater than10 displayed a significantly lower %
of muscular lipids than the others. Thus, A. crassus could be an
additional negative pressure on European eel (specially highly infected
ones) able to hamper transoceanic migration and reproduction.

4.2c The influence of heavy metal and organic pollutants on eel quality

Metallic content was measured in the muscle, the liver and the ovary
samples taken from 80 eels. Each organ was crushed and lyophilised. The
samples were analysed at the University of La Rochelle with the
collaboration of the Centre Commun d'Analyse, under the supervision of Pr
P Bustamante. Mercury was dosed by atomic absorbtion, and 13 metals (V,
Cr, Mn, Fe, Co, Ni, Cu, Zn, As, Se, Ag, Cd and Pb) were dosed using
either and ICPMS or by ICPOES. The contamination levels of persistent
organic pollutants were assessed in collaboration with Claude Belpaire of
the University of Leuwen, Belgium and Adrian Covaci of Antwerp
University. Preliminary results of pollutant analysis show that for 172
eels for which data are available so far, every single eel sampled across
EU catchments was contaminated by PCBs. 38 were heavily contaminated with
loads greater than 300 ng/g (the legal threshold for consumption); 35
were contaminated significantly (contamination greater than100 and less
than 300ng/g), and 101 had contamination levels below 100ng/g. The work
is still in process for other organic and metallic contaminants, but the
results confirm that most eels are contaminated and that very significant
variability occurs within and between sites. Overall, the persistent
organic pollutant (POP) load is very high. The most contaminated eels
occurred in the Scheld catchment (Belgium), followed by the Warwickshire
and Hampshire sites (UK).

The potential detrimental effect of chemical contamination and parasite
load on eel is currently being assessed. For each eel, quality is
inferred from a large range of life history traits derived from biometric
measurements (ie length, weight, eye diameter, pectoral fin dimensions,
girth), estimated age, calculated condition indices (ie, body condition,
fat content, GSI, HSI), and measured hormonal status (11kt). These
factors are considered in the light of life history of each eel (inferred
from otolith microchemistry, and more specifically by Sr/Ca ratio
variations along transects from the core to the edge of the otolith), and
also in relation to parasite loads and chemical contamination. These
characteristics will be combined to provide assessment of the eels'
'quality'. We have now started to test and model effects of these
environmental challenges to propose breeding success indices for
different catchments. As an example, average PCB load does not seem to be
dependent upon weight. However, the minimum PCB load (ng/g) showed a

linear increase with weight, suggesting a baseline relation between body weight and PCB loads in European eels. Moreover, we found significant negative correlations between most POPs and lipid content, age, and gonadosomatic index, strongly suggesting that breeding success of individuals is impacted by contamination even at very low levels. These hypotheses are now being tested with robust statistic modelling.

Outcomes: Peer review paper in submission for the Journal of Parasitology ('Parasite communities effects on spawning migration success and consequences on gene pool contribution of Anguilla anguilla'), peer review paper in submission for the Journal of Animal Ecology ('Are life history traits and quality of European silver eels (A. anguilla) affected by organic and metallic pollutants and parasites?'), peer review paper in submission for the Journal of Fish Biology ('Spatial and temporal variation in the size and age at maturity for the European eel (Anguilla anguilla)'),and a peer review paper in preparation for Aquatic Biology ('First Europe-wide study on the occurrence and impact of the swimbladder nematode Anguillicoloides crassus in silver eels').

4.3 Estimates of silver eel escapement from different catchments

The relative contribution of different European rivers to the spawning (migrating) stock is critically dependent on the overall quality of eels, but also their variability. For example, a river producing a low overall quantity of silver eels, but with a significant fraction of high quality eels may well be contributing more to the spawning stock than a river that produces a higher quantity of eel, but none with the necessary quality to migrate successfully. Catchment- or tributary-level population estimates of eel production often do not take into account the effects of the range of habitats found across the study system, and how these affect silver eel production. The lack of knowledge about eel-habitat relationships precludes the use of this component in population models and limits our ability to predict the silver eel output across catchments. We set out to gather information on the factors that affect the contribution of different catchments by using two different approaches:
a) Assessment of time-series of eel population size
b) Modelling the effect of different environmental constraints on population size and escapement

4.3a Assessing time-series of eel escapement

The size and density of the stock of eels in the Rio Esva in the north-west of Spain has been assessed. Monitoring of glass eels, elvers and male silver eels (females were largely absent) shows a severe fall and a subsequent rise in in-stream densities over a 21-year period. A lengthy period (1989–2000) of synchrony between the decline of glass eels and in-stream density offered strong support for a recruitment dependent stock size hypothesis. A historical minimum in glass eel abundance and in-stream density recorded at the end of the 1990s suggested that the Esva stock was at risk of extinction. However, in contrast to the major decline in glass eel recruitment and a parallel decline in estuarine eels, the density of eels has since continued to increase during the 2000s, to an extent that the Rio Esva stock has recently attained a stock comparable to that recorded in the mid-1980s. Overall, the variations in density of the Rio Esva eels are consistent with the general hypothesis of density-dependent mortality.

The size and density of the stock of eels in the Corrib and Shannon catchments in the west of Ireland has been assessed. The sampling programme comprised collection of biological data on yellow eel population structure, and the collection of biological data on migrating silver eel population structure. Silver eel escapement experiments were performed in three parts of the catchments and compared to historic catch levels. Present day escapement from the Corrib is approximately 36 tonnes (~35% escapement), that is broadly in line with the long-term average. However, there has been and increase in the average size of silver eels and a shift in the sex ratio of silver eels towards females.

New surveys were conducted in 2008/9 in the Loire (one of the largest river systems of western Europe) which currently has no estimate of silver eel escapement. Mark-recapture experiments were conducted to survey the temporal variation of the characteristics of the silver eel population, and compared to similar surveys conducted in 2001 to 2004. Overall, 5231 silver eels were marked, with a recapture rate of 13.4%. A significant negative exponential relationship occurred between daily recapture rates and river flow. The total number of silver eels was estimated using Petersen's calculator for each recapture experiment. An average of 55,000 silver eels was estimated per mark recapture experiment, with the total yearly number of silver eels emigrating from the Loire River appeared to be stable during the 3 first years of the survey with a slight although non significant increase from 352,000 eels in 2001-2002 to approximately 383,000 eels in 2003-2004. However, there was a steep and significant decline in 2004-2005 and 2008-2009, with only 135,000 and 150,000 silver eels respectively.

4.3b Modelling the effect of different environmental constraints on population size and escapement

Despite carrying capacity being one of the most important parameters in population management and modelling of eels, we lack substantial evidence for habitat limitations on freshwater species. Here we tested the ideal free distribution (IFD) hypothesis using spatiotemporal variations in the density of the eels in the Fremur catchment. Almost every site sampled had eels, whatever its location on the catchment and its habitat characteristics. Density estimates (overall mean ± SD of 0.40 ± 0.48 per m2) were at the upper range of other values for European catchments. Moreover, eel densities were mainly influenced by the availability of suitable habitats (rocky substratum and instream cover), which suggests that their distribution reflects an IFD. Despite marked variability in recruitment, the density of the oldest size-class remained stable over the study, suggesting that density-dependent mortality occurred, probably due to intraspecific competition for space and food and to predation. A mixture model used (delta-GLM) enabled to introduce the influence of temporal, macro- and meso-scale habitat factors on eel presence/absence and abundance of 30 sites over an 8-year period. These findings suggest that eel habitats are saturated in the Fremur. Therefore, we suggest that the mean abundance of eels observed could serve as a threshold value for other male-dominated river stocks (provided they have a similar overall percentage of suitable habitats) that are common in small, low gradient streams on the north-Atlantic coast of Europe.

Data on size and age at maturity for male and female European eel (Anguilla anguilla) were gathered from 66 eel stocks belonging to 12 countries during the period 1936-2010. The study is an update of Vøllestad (1992) and brings together new data collected over the

intervening years and made available to ICES / EIFAAC eel working group
and from the EELIAD project. Mean length of female eel increased
significantly with latitude (p less than 0.01), from 500 to 800 mm
between 37-70 degrees of latitude, there was no relationship between male
size and latitude remaining constant at between 380-400 mm. Age at
silvering, increased significantly (p less than 0.01) with latitude from
3 to 25 and 3 to 34 years for males and females, respectively. As
consequence of variability in age and size at silvering, average growth
rate (estimated as size/age) decreased significantly (p less than 0.01)
with latitude for female and male eel. These relationships were modeled
to provide a predictive capability for size and age at maturity for those
river systems where no or little data are available. Trends in silvering
length with time in last 40 years were analysed for three catchments.
Length at silvering in males increased in IJsselmeer (NL) and Girnock
Burn (UK) (p less than 0.01), but not in Burrishoole (IR) (p = 0.66).
Silver eel females were not captured in Girnock Burn, those caught in
Burrishoole show a significant increase in size in Burrishoole (p less
than less than 0.01) while in Ijsselmeer there was no increase in mean
length over the time period (p= 0.07).

Because of their size and behaviour, silver eels are particularly
vulnerable to a range of anthropogenic pressures that can reduce the
numbers of silver eels escaping each catchment. Chief among these
threats are the mortalities induced by fishing pressure and hydropower
turbines. In a case study in the lower part of the River Gudena, we
estimated survival and progression rates of silver eels during the first
phase of the marine migration in the Randers Fjord in Denmark. Fifty
migrating silver eel (total body length: 56 to 84 cm) were captured, and
each was equipped with an acoustic transmitter. Their migration was
subsequently monitored using an array of automatic listening stations,
and progression rate and mortality in the river, inner part of the fjord
and outer part of the fjord were estimated. Survival was high in fresh
water. However, 60% of eels were lost in the inner and outer fjord,
supporting the hypothesis that mortality is large in the early phase of
the marine migration and that fishing may be a major cause of mortality
of silver eels. There was no indication that the slowest-migrating
individuals were more prone to fishing mortality than the faster-
migrating individuals. Progression rate increased as the eels proceeded
downriver and out of the fjord. The migration was predominantly
nocturnal, both in the river and fjord. Based on the available evidence,
a considerable increase in eel survival in the river-fjord system will be
needed in order to fulfil the goals in the European Union recovery plan
for eels.

In a second case study on the effects of hydropower on the Loire, we
developed a model of the timing of eel migration based on environmental
factors. The model is founded on an analysis of a long-term (20 years)
catch time series of professional fishermen of the Loire River (one of
the largest river system in France) and related environmental data. We
used Generalised Linear Models to analyse temporal variations in silver
eel catches. The mixture models used enabled to simultaneously introduce
the influence of meteorological (weather type and nighttime luminosity
index), hydrological (river flow and turbidity) and temporal factors
(number of weeks since the start of the migration period). All the
environmental variables used in the model were standardised to reduce
site and year effects. The analysis revealed that about 80% of the
migration peaks observed can be predicted from the environmental
variables, suggesting that silver eel migration peaks occurred during

predictable environmental windows in the Loire river. Given that most of the variables used in the model are predictable at least at 24 hours in advance, the model provides a tool for managers to anticipate when turbines could be suspended and when spill flows could be provided to protect eels during their downstream migration. This would thereby help to implement the most effective strategy to limit silver eel mortality. We have tested the model successfully on four other French rivers where downstream migration was assessed using Wolf traps (Oir, Scorff, Rouvre, Nive). A new model, Predicteel, has been developed to take some of these concepts further in a management context.

Outcomes: Peer review papers published in Freshwater Biology ('Long-term numerical changes and regulation in a river stock of European eel, Anguilla anguilla'), in Fisheries Management and Ecology ('Infection by Anguillicoloides crassus in a riverine stock of European eel, Anguilla anguilla'), peer review paper published in Aquatic Biology ('Survival and progression rates of large European silver eel in late freshwater and early marine phases'), peer review paper in press in Applied Limnology ('Size and number of male silver eels Anguilla anguilla (L.) in a Cantabrian river over two decades (1990 – 2011)'), peer review paper in preparation for the Journal of Parasitology ('Parasite communities effects on spawning migration success and consequences on gene pool contribution of Anguilla anguilla'), peer review paper in submission for Aquatic Conservation ('Exchange of European eel (Anguilla anguilla) between salinity environments in the Thames river basin'), peer review paper in preparation for the Journal of Fish Biology ('Downstream migration of European eels in the Loire River'),and a peer review paper in preparation for Journal of Applied Ecology ('Predicting silver eel downstream migrations using simple exogenous factor and SARIMAX models').

Potential Impact:

The primary focus of research under the funding instrument 'Activity 6.2.2.1' under sub-heading 'ENV.2007.2.2.1.2 (Ecology of important marine species)' is to 'improve our knowledge of natural resources and to focus this knowledge on their sustainable use'. To this end, EELIAD focuses on improving our knowledge of some aspects of the life history of a species that, even after decades of research, has eluded study. Our aim was to ensure that the biological and ecological data we collected would be integrated into management-relevant models or advice, and to provide recommendations for the management of river catchments. These tools would then be used to contribute to the EU-ERP and assist achievement of the objectives of the EU's Eel Recovery Plan (CEC, 2005).

Potential impact and wider societal implications

Worldwide, eel production (fisheries and aquaculture) is worth over 2 billion EUROS. Eels are the most widely distributed fish species in Europe, and have historic, social and economic significance as subsistence and commercial fisheries. Maintenance of the commercial and artisanal industries in Europe is therefore critically dependent on the sustainability of eel stocks, and on the development of biological knowledge to help define sustainable and justifiable management practices. In addition, eels also play a significant ecological role in freshwater and brackish environments because they are important opportunistic predators at the yellow eel stage, and important prey as glass eels and yellow eels. The combined market and ecosystem services value of eels is therefore considerable.

At the outset of the project, we identified aspects of the research that we predicted would contribute to sustainable exploitation of the European eel stock and therefore have socio-economic and wider societal impact. These aspects are listed below, and are expanded on with explicit recommendations for generating impact at a range of scales, from local to international:
1. Identify spawning areas and marine migration routes;
2. Identify biological and ecological characteristics of eels that contribute to migration success and reproduction;
3. Develop understanding of the stock and recruitment processes of eels;
4. Develop models of European eel productivity and reproductive capability that incorporate variability in life history parameters;
5. Increase public awareness of the unique ecology of eels, their role in EU society, and efforts to ensure their sustainable exploitation.

1 Spawning areas and marine migration routes
The origin of eels and their long-distance migratory behaviour is a source of mystery and controversy. At the onset of the EELIAD project, there was no published information on the natural migratory behaviour of European eels in the ocean, and assumptions and uncertainties in the marine life of eels were numerous. While tracking eels to the presumed spawning area in the Sargasso Sea has not been achieved in the EELIAD project, significant progress has been made in mapping the direction and routes of the spawning migrations of European eels, and in describing and interpreting the stereotypical behaviours of eels over migratory periods of more than 9 months. In addition, factors affecting the migratory success of eels have been identified and include the previously unobserved phenomenon of coastal and oceanic predation. Before the project started, migration studies had been attempted and abandoned after

only a few hours or days. In EELIAD, despite a relatively small investment in tracking technologies, the project has succeeded in tracking eels more than 3000km and to locations close to the mid-Atlantic ridge. The data collected represents an increase of approximately two orders of magnitude greater than that available before the project started. Uncertainties regarding the ability of eels to swim over large distances, of the navigational mechanisms used by eels, and of the range of environments experienced and preferred by eels have been dramatically reduced. The data provided by the tracking programme are a significant and valuable resource that is significantly ahead of current research efforts in the USA and Japan. Research groups in these countries are now looking to draw on the experience and assistance of members of the EELIAD project team to emulate this success. Framework 7 funding of the EELIAD project, and our success in achieving the project's goals, has already been identified as a considerable achievement for European science, and has garnered considerable attention in the scientific community and in the public domain.

(a) We recommend that efforts to map the migration of European eels to their spawning area be continued to resolve remaining uncertainties, and to maintain the research lead over the US and Japanese research areas

2 The biological and ecological characteristics of eels that contribute to migration success and reproduction

Ocean migrating eels show a stereotypical pattern of habitat occupation, moving from deep and cold environments by day to shallower and warmer environments at night. This behaviour was observed in all eels and is likely to be a combination of antipredator behaviours, and navigation or thermoregulatory behaviour. While assessment of the functional significance of the behaviours is ongoing, diel fluctuations in pressure and temperature are a fundamental aspect of the spawning migration of European eel and are likely to be a controlling factor in their maturation and reproductive cycle. Knowledge of this kind will help to develop aquaculture protocols for European eels and, by helping to close the life-cycle and increase aquaculture production, will release pressure on the wild stock.

(b) We recommend that, to assist with the development of aquaculture practices in the EU and to contribute to sustainable exploitation of the stock, experiments are undertaken to test the effect of diel pressure and temperature cycling on eel maturation and reproduction.

Results from tagging studies have shown that heavy predation of silver eels can occur in coastal margins, as well as in the deep ocean. In some years and in some locations, the majority of eels were taken by predators before they were able to escape the continental shelf and occupy the deep ocean. This phenomenon has also been observed in American eels. This predation reduces the number of silver eels escaping to the ocean, and may be regionally and inter-annually variable. Results from tagging studies also showed that a proportion of eels that escape from rivers may not be of sufficient quality to survive the journey to the spawning area. The impact of this knowledge is the revelation of a type of natural mortality in the ocean that is currently ignored in the European Recovery Plan.

(c) We recommend that, to ensure escapement targets are appropriate to sustaining the stock, the influence of at sea predation and natural

mortality on the size of the escaping eel population should be a consideration in setting spawning targets. Further studies with new methods may be necessary to develop an increased understanding of the spatial and temporal dynamics of predation.

There are clear regional differences in silver eels in parasite load and disease, organic contamination, fat content, as well as regional differences in length and weight. However, the influence of physiological and biochemical parameters on migration or reproductive success was not clear and requires further research. Based on the performance of other fish species under similar stresses, however, it is not unreasonable to suggest that eels that are more contaminated, or with a higher parasite load, are of lower quality and reproductive potential than eels with lower contamination levels and fewer parasites. Evidence was also collected that suggests catchment characteristics have a strong influence on biometrics of eels. Integrating information on eel quality collected in the EELIAD project with catchment information being collated under the Water Framework Directive will help identify areas that require additional monitoring or protection. The integrated modelling of silver eel quality and links to habitat type in the freshwater phase will provide valuable information that will reduce uncertainty in defining appropriate management measures. The development of a comprehensive EU wide assessment of silver eel quality is a major achievement and opens the debate on how to incorporate eel quality into escapement targets and monitoring.

(d) We recommend that, to improve management targets, silver eel quality should be included in eel management plans and international stock assessments, either for monitoring purposes, or when setting escapement targets. Further research under laboratory conditions is necessary to identify the influence of quality on reproductive potential and migratory ability.

3 Develop understanding of the stock and recruitment processes of eels
Studies of the genetic structure of eels has reconfirmed that the European eel population is panmictic. The EELIAD project provides the first molecular population genetics study based on the larvae of European and American eel species sampled directly at the spawning grounds, supplemented by analysis of glass eel samples from continental Europe. The analysis provides strong evidence for panmixia in both the Sargasso Sea and across all continental samples. Thus, despite the fact that several recent studies (based on continental samples) have found subtle, but significant, genetic differentiation, we suggest that the European eel should still be considered as a classical (but rare) example of panmixia, and be managed as such. These findings call for management of European eels as a single unit, necessitating conservation and management efforts coordinated at the level of the EU and international community.

(e) We recommend that, to ensure that the focus on integration of national management plans is maintained, the panmictic nature of the eel population is reaffirmed at the next review of the Eel Recovery Plan.

The recruitment index (five year average) is currently at its lowest historical level, less than 1% for the North Sea and 5% elsewhere in the distribution area with respect to 1960-1979. Previous oceanographic modelling studies have led to suggestions that the transport time and mortality of larval eels may be affected by recent changes in the hydrography of the Sargasso Sea, so contributing to this decline. Work

conducted in EELIAD has extended the time-frame of this type of assessment to cover the period of the regime shift in recruitment and, while there is evidence that interannual fluctuations in recruitment will occur as a result of oceanic factors, the scale of the fluctuations is not sufficient to account for the dramatic decline in recruitment. In conclusion, factors that affect eel populations during recruitment and the growth phase remain the most likely to be having an impact, and those that can be influenced. This knowledge helps to reduce the speculation that the decline in eel recruitment is climate, and not anthropogenic, driven.

(f) We recommend that, to avoid unnecessary uncertainty and delay, eel management plans should maintain their focus on factors that can be managed to improve stock status in the growth habitat.

Genetic comparisons among aged silver eels from Northern and Southern Europe did not detect signs of any genetic structure, supporting the notion of a panmictic species (see also 2g, below). An expansion of this data set on silver eels furthermore has allowed for estimation of the genetically effective size of the spawning stock from the late 1980s to the early 2000s. Such annual estimates are expected to provide insights on how the spawning stock size has been related to contemporary trends in continental spawner escapement and glass eel recruitment, and if present escapement targets need to be adjusted to ensure protection of the reproductive capacity of the stock. A comprehensive analysis of trends in spawner population size has never previously been undertaken and will be a significant scientific achievement of direct relevance to management plans.

(g) We recommend that, to continue the integration of scientific evidence into the rational for eel management plans, estimates of the genetically effective spawning stock size should be considered in relation to current escapement targets.

The arrival of glass eels into estuaries and rivers has traditionally supported artisanal and commercial fisheries, especially in the southern European countries of Portugal, Spain and France, and to a much lesser extent the UK and Ireland. Data from these fisheries, and from other fisheries independent sources such as scientific surveys and fixed trapping stations, have been used to construct and maintain recruitment indices that are one of the fundamental evidence bases of the EU eel management plan. However, fisheries are no longer as profitable as they were, and the glass eel industry in Europe is likely to continue only to supply eels for stocking. It is necessary to replace fishery based indices of glass eel recruitment with independent indices. Work conducted in the EELIAD project has provided insight into the environmental factors that contribute to glass eel influxes into estuaries and rivers, and provide a foundation for the design of glass eel monitoring schemes, and the interpretation of data from them.

(h) We recommend that glass eel monitoring plans need to be considered urgently to ensure that time-series of recruitment can be maintained in support of long-term management plans.

4 Develop models of European eel productivity and reproductive capability
Data gathered in the EELIAD project have demonstrated that there are uncertainties associated with the current classification and assessment methods for silver eel status and quality. Accurate classification and

assessment is crucial to determine effective spawner escapement, and work
has progressed in the EELIAD project to refine and improve silver eel
identification protocols. Furthermore, the development of non-invasive
tests for important diseases has proven successful. However, there are
still aspects of eel quality that require either invasive or terminal
tests. The absence of a test for Anguillicoloides crassus has, for
example, inhibited the ability of the EELIAD project to examine
differences in swimming behaviour that may affect infested eels, and
thereby limit their ability to complete the spawning migration.
Unquantified uncertainty is a hindrance to the development and
communication of national eel management plans, and regional differences
in protocol may lead to inconsistencies in how these plans are developed.

(i) We recommend that, to ensure that catchment managers have the
appropriate tools at their disposal to assess eel quality, ICES/EIFAAC
support the rapid development of standardised eel quality protocols
through a series of workshops and provision of an accessible database.

(j) We recommend that, to minimise the potential effect on migratory and
breeding success, management plans for European eels develop plans to
reduce contamination of eels by organic and metallic pollutants.

Results from studies in France, Ireland and Spain that have reconstructed
or monitored long time series of eel population dynamics have shown that
large inter-decadal fluctuations have occurred over the last 25 to 30
years. In part, these fluctuations can be attributed to changes in
fishing effort and catchment management, and they can also be attributed
in part to inter-annual fluctuations in eel recruitment and production,
and inter-decadal changes in the duration of the growth phase. Studies
of silver eel escapement success show that catches peak at times of the
new moon during the months of August through December, that migration to
the sea occurs earlier at more northerly latitudes, and that downstream
migrations are triggered by waterflow and lunar cycle. Losses of silver
eels to fisheries and mortality in hydropower turbines can be
considerable. Developing forecasts of eel runs can help to implement
alert systems to decide when to stop turbines in order to avoid
mortality. However, such systems are not currently operational. Knowledge
of this kind is of benefit because it helps to define the actions Member
States need to take to implement national eel management plans, and helps
to set regional targets for escapement of silver eels.

(k) We recommend that, to develop a full suite of management tools
(including eel run forecasting tools) that are fit for purpose in
delivering the Eel Recovery Plan, long-term monitoring of silver eel
escapement and causes of silver eel mortality will be required with
further integration of models of catchment and eel migration processes.

(l) We recommend that, to minimise the impact of hydropower mortality,
operational research to develop catchment-based forecasting models should
be encouraged to enable integration of Eel management plan objectives
with energy directives.

We compared the behaviour of eels from stocked and unstocked rivers in a
series of tagging experiments using satellite tags, data storage tags and
acoustic tags. The experimental design was to tag equal sized groups of
female silver eels from one location with a record of glass-eel stocking
during more than 20 years and with barriers to upstream migration, and
one group from a river without barriers and without a history of eel

stocking. The experimental groups were released at the same time and place on the Swedish west-coast. The experiment was repeated over two years, the first year with a release in a fjord where the initial behavior could be monitored by acoustic tagging. The results show no statistically significant differences between the groups, nether in the initial behaviour after release, nor in the subsequent offshore migration during several months and over more than 2000 km distances. During the ocean phase of migration there was no difference in the choice of route, depth preference, diurnal behaviour or average migration speed. This new information suggests that eels from stocked rivers may be capable of completing the marine migration, which has previously been suggested as a potential drawback to stocking practices. However, more knowledge is required on a wider range of biological and ecological issues related to stocking.

(m) We recommend that, to reduce uncertainty associated with stocking practices and the comparative performance of eels across a range of criteria, a concerted and coordinated research effort is undertaken to establish the potential and dangers of translocation of eels in support of eel management plans.

5 Increase public awareness of the unique ecology of eels, their role in EU society, and efforts to ensure their sustainable exploitation
The EELIAD eel tracking programme attracted the attention of film and documentary makers in France, Sweden, Ireland, UK, Spain and America. More than 10 short films were made about the scientific work that enabled EELIAD scientists to set the work in its wider context of eel decline. In many cases, this prompted the film makers to seek the input of fishermen and other stakeholders. The mystery of eels provided a powerful story for outreach and disseminating the importance for good stewardship of eels and eel habitat. The project also attracted a lot of written and web-based journalism, and acted as an enabler for scientists to explore and communicate the cultural and societal importance of eels. The EELIAD project helped to build awareness of eels in Europe and generated momentum for their effective management.

(n) We recommend that, to maintain the momentum of the EELIAD project, future outreach should seek to build on the foundation established within the project by further development of the EELIAD website.

List of Websites:
http://www.eeliad.com