Does translocation and restocking confer any benefit to the European eel population?

A review

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Executive Summary:

The European Commission has established an Eel Recovery Plan (ERP) with the objectives of protection, recovery and sustainable use of the European eel stock. To achieve these objectives, Member States have an obligation to develop eel national management plans for each of their river basin districts (RBDs), the objective of which is to provide a long-term escapement to the sea of the biomass of silver eel equivalent to 40% of the best estimate of the theoretical escapement if the stock had been completely free of anthropogenic influences.

One management option identified in the ERP is to stock inland waters with glass eels, elvers or small yellow eels in order to enhance the production of adult (silver) eels, and hence contribute to compliance with a RBD's 40% silver eel escapement target. This management measure is based on the well-founded observation that there is low recruitment (of glass eels/elvers) and depleted populations of growing yellow eels in a large proportion of formerly productive freshwater habitats across Europe, which has led to a reduction in the number of escaping silver eels (e.g. potential spawners) in the European eel population as a whole.

Article 7 of EU COM 1100/2007 requires that any Member State that permits fishing for glass eels/elvers must reserve at least 35% of the catch for stocking purposes within the EU in the first year of a compulsory EMP (which is assumed to be 2010), increasing by at least 5% per year to achieve at least 60% by 31st July 2013. Given the high price of glass eels/elvers on the commercial market (around Euro 350-650 per kg in 2012 and the relative scarcity of glass eels, stocking programmes must be as cost-effective as possible. Furthermore, the benefits of stocking with young eels will not be realised for at least 5-10 years, when the growing yellow eels begin to mature into silver eels.
This review was commissioned by SEG via the Living North Sea project, to provide a synthesis of the available data and information about the instances and effectiveness of re-stocking with eels as a conservation measure to increase the net production of silver eels. The basic question "is there a net benefit of trans-locating eels compared with leaving them to migrate naturally" has been addressed by compiling (mainly) published evidence for the performance of stocked eels in terms of survival, growth and behaviour, as measured in fisheries and experimental studies across Europe. The remit of this review does not extend to evaluation of the availability of eels for stocking, costs of stocking, or the reproductive capacity (in terms of future recruitment) of silver eels. Such issues are, however, touched upon where relevant.

The main findings are as follows:

There is considerable evidence that stocked eels do survive and escape as silver eels, but it is difficult to evaluate whether survival to escaping silver eel is reduced by translocation(to the extent that there may be an overall loss to spawner production). This is mainly because stocking studies have not been accompanied by controls without translocation, though models exist that might provide indicative outcomes. It is, however, logical to assume that enhancing eel populations throughout the species natural range where recruitment has been poor, must increase overall production.

It is equally unclear whether there are differences in the growth rate of stocked and naturally recruited eel that may lead to an overall loss of biomass of escaping silver eel. Even if stocked eels do grow more slowly than native eels (for which there is no evidence), density effects on growth and sex ratio are more likely to influence growth rates and eventual biomass production.

Estimates of the yield that results from stocking with glass eels or small yellow eels have generally been within the range 20-70 g per recruit (4-14 kg per hectare, at a nominal stocking density of 200 glass eels per hectare), though there is obviously a confounding effect on yield of stocking density and potential productivity of the water body into which eels are stocked. This demonstrates that stocking with eels does lead to a quantifiable increase in yield of yellow or silver eel in the stocking location, but we cannot say whether this is an overall increase compared to leaving the glass eels *in situ* (and not catching them for purposes other than stocking).
There do not appear to be any benefits arising from on growing of glass eels in aquaculture facilities before stocking (in terms of overall survival and growth), though holding glass eels with at least maintenance feeding until the time that they can be stocked with a good chance of survival in otherwise cold or ice-bound northern waters is a positive option.

The available evidence shows no clear relationship between stocking density and yield, which probably reflects the variations in stocked waters' carrying capacity for eels and also in the various studies' protocols.

We simply do not know whether changes in the sex ratio of eels as stock density changes represent a risk to reproduction (during spawning), chiefly because the influence of sex ratio at spawning is not known, though it might be presumed that a shift towards females would result in higher overall population fecundity. The default strategy would be to stock in such a way that local densities mirror those that obtained during the period when recruitment was high (1950-1970), if known.

There is good (if indirect) evidence that stocking has resulted in a proportional increase in escaping silver eels, though estimates of effectiveness vary depending on the growth area (fresh, brackish or marine waters) and barriers to emigration.

There is little evidence (but few studies) of any consistent difference between stocked and native eels in somatic (size, fat/lipid content) and reproductive factors (maturation indices, spawning potential) that might result in lower spawning success in stocked eels.

There is insufficient evidence to know whether any behavioural impairments due to translocation that could reduce the success of spawning, though there is evidence that the migratory behaviour of stocked-origin silver eels is similar to that of native eels. It would be prudent, however, to ensure that stocking results in well dispersed eels and only occurs where there are few if any obstacles to sea-ward migration.

As with any translocation of living material, there a risk of spreading of disease and parasites when eels are moved from one area to another. This can be minimised, however, by using glass eels caught by fishing methods that cause the least damage and transporting quickly in conditions that avoid undue stress (density, water quality, temperature). If it is considered necessary to hold eels prior to stocking, it is advisable to start with good quality glass eels (free of parasites and disease, and from areas with low chemical contamination risk) and to use quarantine facilities where eels can be tested, if necessary.

It seems unlikely that the genetic structure of eel populations in recipient waters could be altered by introductions of eels from elsewhere. Current scientific opinion is that the European eel population is essentially genetically unstructured (panmictic), and any genetic variation due to temporal and spatial sub-structuring within recruitment (which is inevitable) is likely to be minimised by stocking either locally (within RBDs or countries, for example) or where eels no longer recruit naturally (but growth and escapement opportunities are good).

Despite a considerable body of information, there are no clear answers to the issues mentioned above, chiefly because very few studies have been carried out in a controlled way. Nevertheless, the results of this review can be regarded as setting a benchmark derived from the scientific evidence available up to May 2012. This enables us to challenge what we do and do not know about the benefits of stocking with eel, to make decisions about the most rewarding focus of new work, and to judge new results as they become available.

To help future decisions, documented assessments of the risks of stocking should be carried out (with explicit scientific input), both to judge whether stocking should take place and to assist with post-stocking monitoring. This should aim to assess whether stocking has been successful in achieving its objectives (usually lacking) and, if adverse effects of stocking are encountered, to guide corrective measures.

Where stocking continues, this review suggests that there are advantages of stocking with glass eels/elvers because of the larger numbers available (though in a limited season), that have not been subject to local density-dependent and habitat influenced mortality, lower risk of disease and parasite transfer, lower transportation costs, and lower impact on local donor populations at recipient sites. The advantages of stocking with small yellow eels (wild-caught) are a lower mortality after stocking, a more predictable outcome, shorter time before spawning escapement and, possibly, later relocation could facilitate seaward migration.

With respect to ICES' concern that stocked/trans-located eels experience impairment of their navigational abilities, this review has provided evidence that stocked eel will, in productive environments, produce yellow and silver eels that will attempt to migrate. As yet, however, no eel, let alone one of stocked origin, has been followed to the spawning grounds, and we do not yet know whether there is any net benefit of translocation and restocking to the next generation of glass eels compared to leaving glass eels to recruit naturally.

This does not mean that there are no benefits to be gained from stocking. As long as there is substantial recruitment of glass eels to estuaries from which they are prevented from ascending local rivers because of permanent barrages, catching and trans-locating them with minimal mortality to productive habitats, from which they can escape back to the sea, must be a beneficial option. A less quantifiable option, that might benefit the species by ensuring diversity in the spawning population, is to stock European eels in those parts of their natural range where there is currently no or little recruitment and where phenotypic variation can be maximised (warm saline lagoons in the eastern Mediterranean; cold freshwater lakes in Scandinavia, for example).

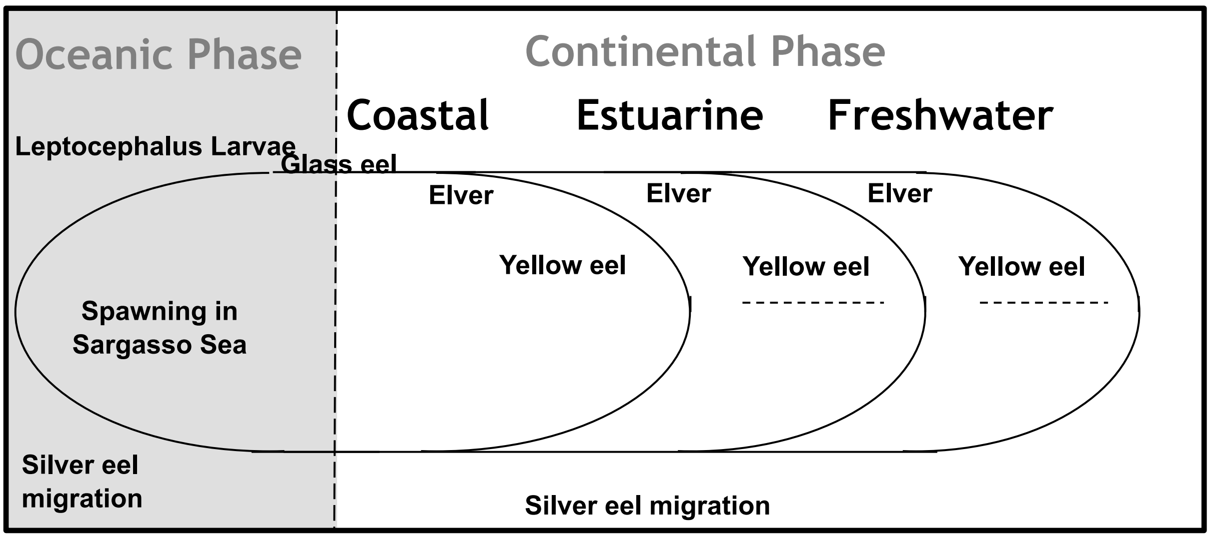
Two areas for future research have been highlighted by this review. First, the use of quantitative population models to investigate the yield of silver eels from stocking compared to leaving glass eels to recruit naturally (the control situation). Second, further examination of the reproductive fitness of silver eels originating from stocking compared to native-origin eels, and the migratory behaviour and capability to reach the spawning grounds of eels in northern and southern continental Europe, north Africa, the eastern Mediterranean and along the Atlantic coast.

Introduction and background to this review

Recruitment to the European eel (*Anguilla anguilla*) population has declined since the 1970s to levels that are considered to be unsustainable unless strong conservation measures are introduced (ICES, 2011a). Data complied by the Joint European Inland Fisheries Advisory Commission (EIFAC)/International Council for the Exploration of the Seas (ICES) Working Group on Eel (WGEEL) indicate a downward trend in the numbers of glass eels being recruited to European waters since the high levels of the 1970s. In England and Wales, for example, commercial glass eel catch data indicate recruitment has declined by 75–90% since the 1980s, tending to stabilise in the late 1990s and showing some recovery in western regions in 2010 and 2011 (Walker *et al*., 2011). Declines elsewhere in Europe appear to have been more severe and to have occurred earlier in more northerly Scandinavian and southerly Mediterranean areas (Knights *et al.,* 2001; ICES 2011b). The factors that may be responsible for this recruitment decline include overfishing, pollution, disease and parasites and other freshwater habitat constraints (drainage, barriers to migration, hydro-power turbines etc), though there may also be a contribution due to changes in Atlantic currents affecting the trans-oceanic migration of leptocephali (Kettle and Haines, 2006; Bonhommeau, 2009). Oceanic factors are also implicated in the decline in recruitment of the American eel *Anguilla rostrata* to North America in recent decades, which has followed a similar trend to that of *A. anguilla* in Europe (Symonds, 2007).

Before proceeding further, it is useful to remind ourselves of the life cycle of the European eel and particularly of the freshwater life stages that are the most susceptible to anthropogenic influence, and where measures to conserve the species are directed (Figure 1). Leptocephalus larvae, most probably derived from spawning in the Sargasso Sea, are carried eastwards by currents for two or three years across the North Atlantic Ocean towards the coasts of western Europe, the Mediterranean and North Africa (McCleave, 1993; Bonhommeau, 2009) and, on reaching the continental shelf, metamorphose to the unpigmented glass eel stage. They enter estuaries when temperatures rise above 4-6°C; in the winter in the Bay of Biscay and more southern areas and in spring in Britain (Naismith and Knights 1988; White and Knights 1997). Major glass eel runs still occur into the Atlantic-facing estuaries in North Africa, Portugal, Spain, France and the UK (the most important fisheries for glass eel are in French estuaries in the Bay of Biscay and the Bristol Channel and Severn Estuary), probably because of the more favourable position of the west coast relative to Atlantic oceanic migration pathways (Knights 2002). Glass eels settle out of the water column and metamorphose into pigmented elvers around the point of tidal reversal in estuaries.

Figure 1. The European Eel Life Cycle (from Williams and Aprahamian, 2004)



The elvers may remain and feed in coastal marine or estuarine waters or begin active upstream migration in freshwater, where they disperse to feed and grow for up to 20 or more years as yellow eels before maturing into silver eels, at which stage they migrate back to the oceanic spawning grounds. Sex determination in eels takes place during the growing phase, and appears to be influenced by density and growth rates. This process is discussed more fully later, but suffice it to say here that age (usually expressed as time after transformation from glass eels into elvers) at silvering may range from 2-4 years in Mediterranean waters to 40+ years in cold Scandinavian waters, and is earlier for male eels than for females. The population dynamics of eels is also discussed later in relation to evaluation of the processes that determine the production of seaward-migrating adult silver eels from glass eels, though it is pertinent to mention that current scientific thinking is that European eels comprise a single panmictic stock, i.e. there is no significant genetic structuring within the population (see Genetics).

Eels are ubiquitous in their distribution, being found in all types of fresh, brackish and coastal waters, and the European eel is most active at temperatures above 14-16°C and relatively inactive when temperatures fall below 5-10°C, commonly remaining in burrows during winter, often in deeper water where conditions remain more constant (Tesch 1977; White and Knights 1997a). Eels are carnivores, feeding on a wide range of invertebrates and fish, and have a relatively high energy value, especially as they build up fat reserves for over-wintering and as they mature ready for migration back to the Atlantic Ocean (Tesch 1977; Knights 1982).

Nomenclature

There are numerous names for the various life stages of the eel (even in English), and these are not necessarily used consistently in the studies and investigations upon which this review is based. In order to assist clarity, therefore, I have used five named life stages to cover the range of names used. These are:
Leptocephalus larvae – oceanic pelagic stage prior to glass eel;
Glass eel - unpigmented coastal stage (first fished stage);
Elver - pigmented stage found in estuaries and lower river reaches (the distinction between glass eel and elver is not clear cut);
Yellow eel – the juvenile, feeding stage in coastal, estuarine and fresh water, small individuals of which are sometimes called bootlace or fingerlings (possibly prior to sexual differentiation);

Silver eels – which have stopped feeding and have maturing gonads, and migrate as adults back to the oceanic spawning grounds.

Conservation of eels

The substantial decline in recruitment (in particular) prompted ICES to advise the European Commission that the European eel stock is outside safe biological limits and that its fishery is not sustainable (ICES, 2001). The most recent assessment of the European eel's status (ICES, 2011b) indicates that the overall stock decline continues. Overall glass eel recruitment has fallen to 5% of the 1960–1979 average in the Atlantic region and to less than 1% in the continental part of the North Sea region and shows little sign of recovery, though catch rates in some UK and France glass eel fisheries appear to have increased in the last three years. As a consequence, the abundance of young yellow eel in many areas has also declined and, put bluntly, the eel stock is in a critical state. In 2007, European eel was included in CITES Appendix II that deals with species not necessarily threatened with extinction, but for which trade must be controlled if it is necessary to avoid utilization incompatible with the survival of the species. The listing was implemented in March 2009. The European eel was listed in September 2008 as 'critically endangered' in the IUCN Red List (IUCN Red List website).

In response to scientific advice and stakeholders' concerns about the plight of the European eel, the European Commission established a management framework in 2007 through an Eel Recovery Plan (ERP: EC Regulation EU COM 1100/2007; "Establishing measures for the recovery of the stock of European eel": EC, 2007), with the objectives of protection, recovery and sustainable use of the stock. To achieve these objectives, Member States have an obligation to develop eel management plans (EMPs) for each of their river basin districts (RBD). The objective of the national EMPs is to provide, with high probability, a long-term escapement to the sea of the biomass of silver eel equivalent to 40% of the best estimate of the theoretical escapement in pristine conditions (i.e. if the stock had been completely free of anthropogenic influences). Lacking analytical assessments of the population dynamics for European eel (which are available for many commercial marine teleost fish species, and salmon, for example), this target is based on the general principle that a fish stock is likely to remain sustainable if its abundance does not fall below a particular level compared to its unexploited state. Readers wishing to explore this rationale further are refereed to the Commission's report (EC, 2007). Where RBDs are not meeting these biomass targets, Member States are required to take action, including to reduce anthropogenic mortalities in order to increase silver eel biomass.

One management option identified in the ERP is to stock inland waters with glass eels, elvers or small yellow eels in order to enhance the production of adult (silver) eels, and hence contribute to compliance with a RBD's 40% silver eel escapement target. This management measure is based on the well-founded observation that there is low recruitment (of glass eels/elvers) and depleted populations of growing yellow eels in a large proportion of formerly productive freshwater habitats across Europe, which has led to a reduction in the number of escaping silver eels (e.g. potential spawners) in the European eel population as a whole. This lack of recruits is, in part because of the aforementioned decline in overall recruitment, but more specifically because of constraints on migration (physical or chemical barriers) or geographical location well away from those areas where recruitment of glass eels is still relatively good, essentially the west coast of Europe: France, the UK and Ireland.

Article 7 of EU COM 1100/2007 requires that any Member State that permits fishing for glass eels/elvers (defined as eels < 120 mm totlal length, used throughout) must reserve at least 35% of the catch for stocking purposes within the EU in the first year of a compulsory EMP (which is assumed to be 2010), increasing by at least 5% per year to achieve at least 60% by 31st July 2013. The price of glass eels/elvers on the commercial market peaked at over Euro 250 kg^{-1} in the late 1990s, driven up by high demand for seed stock for eel farms, especially in China (Knights *et al.,* 2001) and, although prices were about Euro 70-110 kg^{-1} on the European market in 2000, they have again increased considerably, to around Euro 350-650 kg^{-1} (depending on time of season) in 2012 (P. Woods pers. comm.). Fisheries providing eel for stocking will, therefore, require significant funding and, given the relative scarcity of glass eels, stocking programmes must be as cost-effective as possible. Furthermore, the benefits of stocking with young eels will not be realised for at least 5-10 years, when the growing yellow eels begin to mature into silver eels.

The purpose of this review and its structure

This review was commissioned by the Sustainable Eel Group (SEG) via the Living North Sea project (LNS), with the objective to provide a synthesis of the available data and information about the instances and effectiveness of re-stocking with eels as a management tool. It will be submitted to the European Commission Directorate-General for Maritime Affairs and Fisheries (DG MARE) in support of their assessment of the reports from Member States on their national EMPs.
The review is based largely on information obtained through scientific research, either published in peer-reviewed journal papers (and, therefore, of assured quality) or technical reports (which may be no less authoritative, but may have not been externally scrutinised)

and, to a lesser extent, from other written communications that may contain opinion (rather than fact) to a greater or lesser extent. In the latter cases, where used, I have only included information that can be verified or appears to follow a logical argument. I have also indicated, where relevant, work that is in progress or currently unpublished, which may inform the debate in the near future. Subsequent to the first draft of this review being prepared, a substantial body of information was presented orally and as posters at the 6th World Fisheries Congress, held in Edinburgh in May 2012, which reveal the most recent advances in eel science. Though they are only currently available as abstracts (indicated as WFC, 2012), I have very briefly summarised those that were most relevant to this review (and provide new insights), both to inform and to act as a pointer for forthcoming publications on the subject.
The report is written with a wide range of stakeholders in mind, from dedicated scientists working on eel biology and population dynamics in relation to anthropogenic impacts (fishing, habitat destruction, turbines etc), through management and conservation bodies, organisations and administrations, to those with a more direct involvement with eels (fishermen and aquaculturists). It is intended that this report should be accessible to all these people, and the basis for its findings should be as explicit and traceable as possible. For this reason, I have followed scientific publishing practice in the body of the report, dealing with each issue (see contents list) in sections, in each of which the sources of evidence are indicated by citing publications (elaborated in a bibliography) and finishing with a summary of the main findings, written non-technically as far as possible and clearly indicating what we do and do not know. These findings are further discussed in the review's conclusions, and summarised in an Executive Summary at the start of the report, for those who wish to quickly appreciate the main outcome of the review.

Where possible, the examination of evidence for the success or other wise of stocking has been structured regionally, partly in order to group information from studies carried out in similar environmental circumstances, but also because the results vary to the extent that they may not be applicable between regions. For this purpose, studies are grouped by Atlantic coast, Mediterranean, Scandinavia and mainland Europe (away from the Atlantic coast), plus north east America, where the American eel *A. rostrata*, shares a common spawning and oceanic larval migration route with *A. anguilla*. With few exceptions (particular information on biology), I have restricted this review to these two Anguillid species.

Scientific advice on stocking with eels: scope of this review

As the main source of scientific advice to the European Commission on the conservation of the European eel stock and management of its fisheries, ICES advice has displayed a somewhat ambivalent attitude to stocking with eels, which was first proposed at a joint EIFAC/ICES Symposium in 1976 (Dekker *et al.,* 2007). In 2006, WGEEL (ICES, 2006) noted that scientific advice on stocking with eels has changed over the years, from being in favour (Moriarty and Dekker, 1997) to a more precautionary stance that reflected the potential risks associated with disease transfer and/or genetic impacts (ICES, 2000). With the continuing decline of recruitment and poor stock status, however, WGEEL (ICES, 2006) presented a more pragmatic argument for stocking, realising that the decline in glass eel recruitment was limiting the options for restoring the stock. WGEEL (ICES, 2008) updated stocking figures and practical information to support best practice in stocking, and estimated that the recent European glass eel catch (circa 50 t in total, P. Woods pers comm.) was less than that required (up to 1000 t) to supply the potential productive habitat (about 40,000 km^2) within the species' natural distribution range, and suggested that stocking alone is unlikely to achieve the EU's eel recovery objective in the medium term. The availability of glass eels for stocking varies considerably between countries. In the UK, for example, glass eel catches are much less reduced than elsewhere in Europe, and management options such as reducing exploitation probably provide less scope to improve production and escapement of silver eels than in other parts of the European eel's natural range. Where recruitment

potential remains high, removing or by-passing upward and downward barriers will have a greater effect on production than other areas where recruitment has declined to a level insufficient to fully utilise the habitats restored by passes. WGEEL emphasised that the priority for managers is to make best use, in stock enhancement terms, of a scarce resource, and that eel stocking should be performed in the most efficient manner.
The most recent advice from ICES, in November 2011 (ICES 2011a), was that the status of eel was considered to remain critical and all anthropogenic mortality (e.g. recreational and commercial fishing, hydropower, pollution, tidal and flood defences, navigation weirs, destruction of habitat) affecting production and escapement of eels should be reduced to as close to zero as possible, until there is clear evidence that both recruitment and the adult stock are increasing. ICES also reiterated its concern that glass eel stocking programmes are unlikely to substantially contribute to the recovery of the European eel stock, but did suggest that all catches of glass eel should be used for stocking where survival to the silver eel stage and escapement to the ocean are expected to be high (to facilitate stock recovery).

In line with ICES advice, and given the relative scarcity of glass eels throughout Europe, it is imperative that the most effective approach ('best practice') is identified as soon as possible to maximise the benefit of stocking in terms of silver eel escapement. It is also important to understand whether stocking with eels translocated from one site to another will actually produce a net benefit in terms of silver eel escapement, compared with leaving the eels to find their own way into their "natural" habitat. This is essentially the purpose of this review, which seeks to address the apparently simple question "is there evidence that translocating eels has resulted in a net benefit to the European eel population?" There are wider issues, of course, which include biodiversity (eels have been "key" species in many ecosystems) and variability within the eel population itself, but these are subsidiary considerations in the present review.

It is not intended here to explain the scientific basis for stocking as a management tool, nor to address the associated legislative or political questions (whether fisheries on glass eel should continue to operate, for example), or to examine whether a surplus of glass eel really does exist in some localities (e.g. the Severn Estuary, Bay of Biscay). Furthermore, the review does not seek to evaluate the benefit to fisheries of stocking (either for the donor glass eel catchers or subsequent yellow or silver eels catches), though this is clearly relevant in terms of silver eel production. It is presumed that any consideration of whether and where to stock with eels is based on: 1. the need to enhance local silver eel production under EMPs and 2. the likelihood that production and escapement of silver eels (and ultimate reproductive success) from a particular water body will be increased by stocking.

It is important to be clear what we mean by "stocking" (or "restocking"). Authors have used terms such as "translocation" and "redistribution" when they are referring to the anthropogenic movement of glass eels or older life stages from a natural source (the "donor" site, to which glass eels/elvers have migrated naturally) to an area in which recruitment is thought to be reduced (for whatever reason) and where it is presumed that the local yellow and/or silver eel population is depleted. In this review, all such movements of eels will be termed "stocking", whether the translocation is within a particular catchment, for example, by catching glass eels or elvers in the estuary or lower river and re-distributing them upstream of otherwise impassable obstacles (barrages, dams, weirs), or trans-locating them between catchments or, indeed, countries. In this context, eels that have been caught and translocated (direct, or via aquaculture) will be termed "stocked", whilst eels that recruited naturally to growing areas will be termed "native". They are all essentially "wild" – aquaculture has not yet found a reliable way of breeding European eel, so none are farm-bred.

In the context of the present review, it is not important whether the aim of stocking in the past has been to enhance yellow or silver eel stocks for commercial exploitation, for biodiversity or for eel conservation reasons, provided evidence is presented on the success or otherwise of stocking in boosting numbers or biomass of escaping silver eels (or which would result if exploitation was curtailed). The main issue to be addressed is how and whether we can evaluate the success of stocking. Put simply: will more silver eels be produced by trans-locating eels rather than leaving them *in situ*. The main questions to be addressed are:

- Is **survival** of stocked eel to escaping silver eel lowered (to the extent that there may be an overall loss to spawner production)?
- Are there differences in the **growth rate** of stocked and native eel that may lead to an overall loss of biomass of escaping silver eel (to the extent that there may be reduced spawner production)?
- Is there evidence that stocking with eel actually leads to an overall increase in **yield** (of yellow or silver eel)?
- Does **on growing** in aquaculture facilities before stocking confer any benefit?
- How does stocking density influence the above?
- Might changes in the **sex ratio** of eels as stock density changes represent a risk to reproduction (during spawning)?
- Do stocked eels actually contribute to spawning escapement?
- Are there differences in somatic (size, fat/lipid content) and reproductive factors (maturation indices, fecundity) that might result in lower spawning success in stocked eels?
- Are there **behavioural** impairments (e.g. migration, spawning) due to translocation that could reduce the success of spawning?
- Is there a risk of spreading of **disease** and **parasites** when eels are moved from one area to another?
- Could the **genetic** structure of eel populations in recipient waters be altered by introductions of eels from elsewhere?

Previous reviews of eel stocking

The most recent review of information on eel stocking was carried out in 2011 by WGEEL (ICES, 2011b). WGEEL has evolved over the decade or so since the original EIFAC/ICES Eel Study Group managed to convince the EC and the wider community that the European eel population was in serious trouble, and its participants now include well-informed eel scientists from all relevant countries. Their combined expertise is, therefore, comprehensive and includes first-hand knowledge of work in progress (though WGEEL reports can be restricted by the specific terms of reference obtaining at any one annual meeting). Stocking and transfer of juvenile eel was discussed at length by WGEEL (ICES, 2006, 2007 and 2008), covering the principles and extent of stocking, stock transfer practices and their contributions to fisheries. The effect of these activities on silver eel escapement has been discussed mainly from a conceptual and theoretical viewpoint, principally due to a lack of hard data and the absence of a predictive model. In 2011, however, WGEEL examined what is known about the effectiveness of stocking in increasing silver eel production and escapement, as compared to the traditional use of stocking to support fisheries. Several local studies were identified that showed that stocking has enhanced the yellow and silver eel stocks in a number of water bodies (lakes in Denmark, Germany, Sweden and Estonia, Northern Ireland, as well as Danish streams and marine areas). Interestingly, WGEEL concluded that the performance of stocked, on-grown eel cannot be assumed to be as good as that of natural immigrants, though it does often fall within the ranges of best and worst observations of performance of native stock (once they have reached the yellow eel phase, presumably). ICES (2011) also includes an evaluation (largely through modelling predictions) of the efficacy of stocking in producing spawner biomass output, as a means to improve the scientific basis for advice on the management of European and American eel. This raises an important question: can we evaluate the success or otherwise of stocking without using analytical models (see section on determining net benefit of stocking)?

A literature review of migration patterns and orientation in stocked eels, conducted by Wickström *et al.* (2010), focussed on the orientation, navigation and migration of silver eels of stocked and native origin in studies conducted in and around the Baltic Sea. They also looked at the growth and survival of stocked eels in comparison to natural immigrants, suggesting that there is no controversy on this point between scientists or managers (inferring that they are similar between stocked and native eels). This review is connected to the EELIAD project, a minor objective of which is to investigate whether there are any behavioural differences between eels which immigrated naturally or were stocked. Preliminary results from this project are discussed later.

In anticipation of the implementation of the stocking option in national EMPs, the Environment Agency of England and Wales commissioned, in 2009, a review of the (potential) effectiveness of a programme "to redistribute some part of the available stocks of glass eels and elvers to suitable habitats throughout England and Wales to maximise survival to adult and thus maximise the adult stock emigrating to spawn successfully". Solomon and Aprahamian (2009) noted that the practice of stocking lakes and rivers with glass eels, elvers and small yellow eels has been employed for many years throughout most of the range of the European eel, with the focus in most cases on achieving higher fishery catches of yellow and silver eels in the receiving waters (rather than enhancing the eel population *per se*). The authors found that most stocking programmes and assessments have been based upon lakes, possibly because yellow and silver eels can be more efficiently exploited and monitored there through fisheries' catches. They did not conduct an exhaustive review of all stocking programmes, but selected information that they considered useful to address the issues arising from stocking in England and Wales from the point-of-view of eel conservation.

A complementary report, on developing guidelines for best practice in stocking eel for enhancement purposes, was prepared for the UK (England and Wales) Marine and Fisheries Agency (Walker *et al.,* 2009). This reviewed several manuals and reports on the theory and practical approaches to stocking (e.g. Williams and Aprahamian, 2004; Symonds, 2006; Williams and Threader, 2007) and evaluations of the outcome of stocking by WGEEL (ICES 2006, 2008 and 2009a). This report also presents a review of published and grey literature, and discussions with scientists and aquaculturists engaged in stocking and rearing eel, with the aim of identifying indicative value ranges with which to parameterise and develop a 'simple' model of eel population dynamics and production (ESAT, see Determining net benefit of stocking). The analysis of some of the available data in order to elucidate particular features of eel population dynamics is relevant to the current review.

Symonds (2006) presents a comprehensive review of knowledge on eel stocking as a way to enhance local and regional populations and spawning stock biomass of the American eel (*A. rostrata*). This was carried out on behalf of South Shore Trading Co Ltd, New Brunswick, which collects and cultivates glass eels to supply the world-wide eel market, and was motivated by a government proposal to use stocking to increase the number of wild eels in Canada. Symonds (2006) also discusses stock enhancement as a fisheries management strategy and attempts to identify the knowledge gaps, risks and uncertainties associated with eel stocking as an enhancement tool.

Williams and Aprahamian (2004), updating the review of Knights and White (1997), noted that most of the information in the literature comes from empirically derived input-output models, i.e. where stocking strategies and rates are compared to fishery catch returns. For example, there are good data for the Lough Neagh fishery in Northern Ireland (Allen *et al.*, 2006). Williams and Aprahamian (2004) found few attempts to study and monitor stocking into rivers (e.g. Aprahamian, 1986, 1987; Berg and Jorgensen, 1994), and fewer still that report long-term assessments of the production of eels in rivers (e.g. Vollestad and Jonsson, 1988). They concluded that recapture rates of stocked eels (in fisheries) appear to be low, often below 5%, unless silver eels can be efficiently trapped on their seaward migration.

These reports together provide a solid foundation for the present review, which seeks to identify papers and reports that are relevant to the task in hand, and to summarise and present their findings as meaningfully as possible. Given the eel's ubiquity throughout

Europe and its economic importance to fisheries in many countries, it is striking that most of the work that is germane to this report has been carried out in relatively few areas. Together, Germany, Sweden and Poland account for the vast bulk of knowledge on the success or otherwise of stocking and the potential for stocked-origin silver eels to contribute to spawning and future recruitment.

A brief history of stocking with eels

The most recent report of WGEEL (ICES, 2011) suggests that stocking with glass eel in Europe as a whole reached a peak between 1960 and 1988, but then decreased rapidly and appears presently to be at a very low level (Figure 2). There appears to have been a contemporary increase in the number of small yellow eels stocked since the late 1980s (Figure 3). In most historic cases, stocking with eels has been to support fisheries in areas where natural recruitment is relatively poor (either due to distance from the Atlantic or barriers to migration).

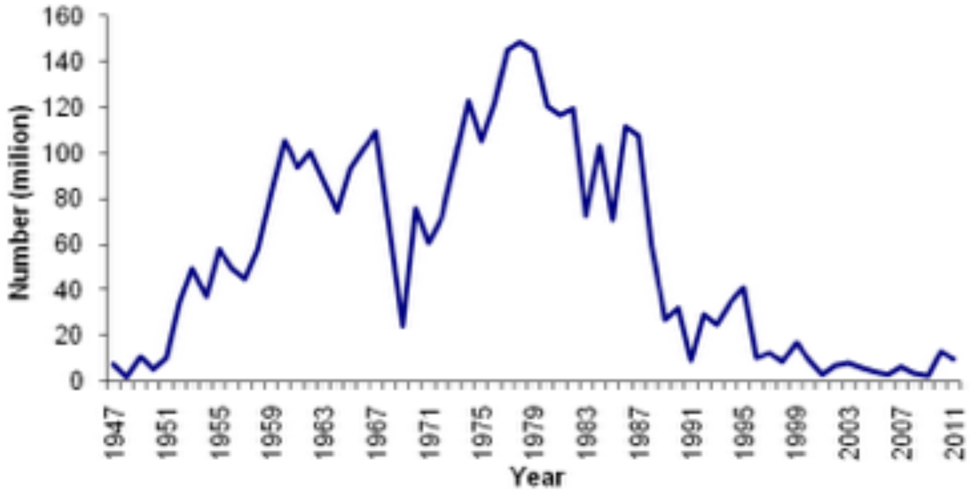


Figure 2. Stocking of glass eel in Europe (Sweden, Finland, Estonia, Latvia, Lithuania, Poland, Germany, the Netherlands, Belgium, Northern Ireland, France and Spain), 1947 – 2011 (source ICES 2011b).

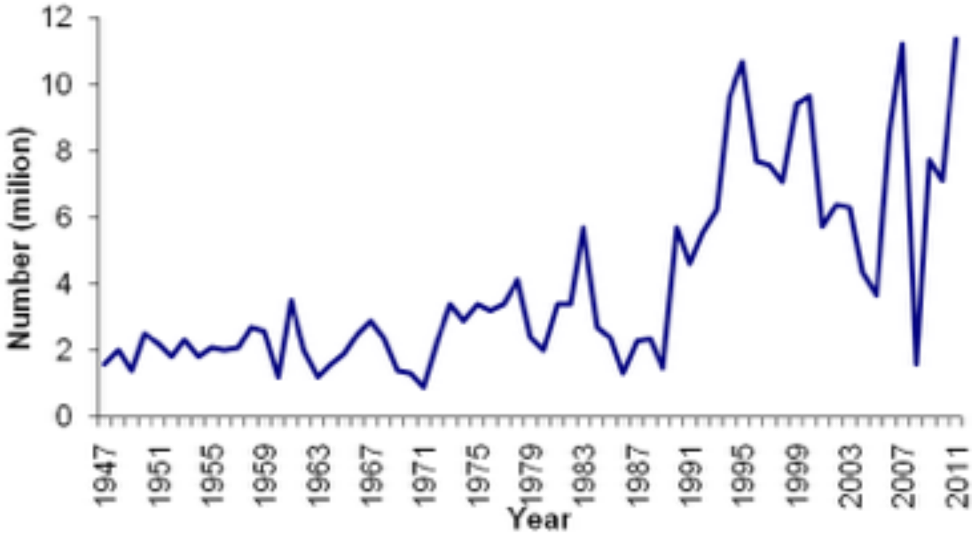


Figure 3. Stocking of small yellow eel in Europe (Sweden, Finland, Estonia, Latvia, Lithuania, Poland, Germany, Denmark the Netherlands, Belgium, and Spain), 1947 – 2011 (source ICES 2011b).

ICES (2011) also provides an indication of the amount of stocking with glass eels and small yellow eels being carried out at national level in accordance with national EMPs, summarising the available data by country, up to 2010 and partly for 2011. Moving south and west from the most distant stocking locations (in relation to sources of glass eel, and where data area available):

Finland: In 2011, 200 000 individual eels were stocked (EMP).

Sweden: only imported and quarantined glass eels have been eligible for stocking since 2006 (supported with public money) and, from 2009, all glass eels are marked with $SrCl_2$ in their otoliths. Since 2010, glass eels are imported exclusively from the Bay of Biscay (Charente-Maritime in France). (Sweden has used quarantined eels for stocking since 1984, and Scandinavian Silver Eel has been involved in stocking roughly 28 million in Sweden and 12 million in the rest of Europe. R. Fordham pers. comm.).

Estonia: Historical data are available on stocking of glass eel/young yellow eel in Estonia since 1950. In 2011, 680 000 glass eels (of UK origin) were stocked (EMP).

Latvia: Historical data of stocking from 1945–1992 are available and, since 1992, all stocking in natural water bodies in Latvia must be reported. In 2011, 100 kg of glass eels (from the UK) were stocked in the River Daugava and basin lakes connected with Gulf of Riga (EMP).

Poland: About 6 t of small yellow eels (average weight 5 g) were stocked in August 2011 in various water bodies (EMP).

Germany: There is no central database on stocking, but some data are available within states. (extensive stocking with glass eel from the UK started in 1907. P. Woods pers. comm.).

Denmark: There has been a national stocking programme since 1987 to enhance eel populations in both inland and marine waters. The stocking material is glass eel imported mostly from France by Danish eel farmers and further grown in heated culture to a weight of 2–5 g before they are stocked.

Netherlands*:* Glass eel and young yellow eel have been used for stocking inland waters for centuries, mostly by local action of stakeholders.

Scotland: No eel stocking currently takes place.

England and Wales: About 37 kg of glass eel (UK origin) were stocked in rivers of England and Wales in 2010.

Northern Ireland: In 2010, 996 kg of glass eel were stocked, originating from fisheries in Northern Spain and the west coast of France.

Republic of Ireland: No stocking of imported eel takes place.

France: The first nationally organized stocking of glass eel started in 2010 in the Loire River, and will continued in 2011.

Spain: no stocking on a national level. Each autonomic region manages its own stocking.

Portugal*:* no eel stocking at national level.
No data are available for **Lithuania, Belgium** (though glass eel stocking is proposed (EMP) for Flanders), **Italy** or **Morocco**.

This information can be updated once the stocking data have been provided to the Commission by Member States in their EMP reports (expected July 2012) or when WGEEL updates the above (available in November 2012).

WGEEL (ICES 2011b) observes that the lack of traceability systems (currently only operating in France and the UK) and poor data reporting makes it difficult to provide accurate information on the quantities of glass eel used for stocking. However, WGEEL estimated that European glass eel fisheries in 2011 sent 12% of their total catch for stocking (presumably within the stocking option under the EU eel Regulation EU COM 1100/2007), and 30% to aquaculture, with fate of the remaining 58% unknown. Note that the proportion of the glass eel catch of any Member State that permits fishing for glass eels/elvers made available for stocking should typically have reached 40% in 2011. Throughout this review, a glass eel is assumed to weigh 0.33 g, i.e. some 3000 individuals per kg.

Sourcing eel for stocking

It is not within the remit of this report to evaluate the availability of a surplus of glass eels or older stages for stocking, but there are a number of accompanying factors that have a bearing on the success or otherwise of stocking. WGEEL (ICES, 2006) warned that, at low stock levels, removal of glass eel from any site to stock another should only be done with a

full assessment of the effect on recruitment into the productive areas naturally dependent on that donor site. ICES (2008) summarises information on how managers might assess whether a surplus of glass eel exists (and can be taken for stocking without detriment to the yellow eel population and silver eel escapement in the donor catchment), and quantification of this surplus. It is unlikely that this has ever been done in practice. The availability of glass eel for stocking (or aquaculture) depends almost entirely on the existence of a glass eel fishery, and is regulated by the EU Eel Regulation (EC, 2007) and indirectly also by the trade restrictions imposed by CITES (CITES, 2008), though this does not apply to movements between Member States within the European Community. The availability of sufficient quantity and quality of stock fish and suitable methods of transportation were also considered by Symonds (2006) and Williams and Threader (2007). Bark *et al* (2007) discuss the availability of glass eels in England and Wales and, although Briand *et al* (2005) estimated that a surplus in the river Vilaine, Briand *et al.* (2007), Beaulaton (2008) and Briand (2009) suggest that there may no longer be a local surplus of glass eels along the French coast.
Knights *et al.,* (2001) discuss the habitat conditions to be considered for selecting sites from which to source eels for stocking, and Williams and Aprahamian's (2004) report contains a section that considers issues such as: source of eel, health of the stock, handling and transportation to stocking site, stocking densities, age and size of stock, timing of stocking and mechanisms of release, all of which must be taken into account when trying to maximise the benefits and minimise potential risks (Cowx, 1998). Williams and Aprahamian (2004) concluded that glass eels are the most cost-effective source of stocking material in terms of returns equivalent to stocking with yellow eel. They observed that the distance between source and stocking site will have implications for transport stress, environmental dissimilarities and the possible interference with navigation of the adults returning to sea.

Allen *et al.,* (2006) and Rosell (2009) compared the effect of stocking with glass eels of different origins into Lough Neagh in Northern Ireland, either sourced from the estuary of the River Bann (which drains Lough Neagh) or from the Severn Estuary in England. Their model shows that eel catches based on stock from the Bann Estuary can be up to three times higher than when stocking with Severn-origin glass eels, and they suggest that the latter could have a reduced ability to survive and grow (possibly due to stress associated with translocation, though transfer mortalities from the Severn Estuary to Lough Neagh have been as low as 0.25% - P Woods, pers. comm.). Nevertheless, WGEEL (ICES 2006) noted that the additional stocking (with Severn-origin glass eels) in the period 1984 to 1989 shows clearly in maintained catch rates in the period 1999 to 2005 and, given the known escapement of silver eels from the Lough Neagh system (Rosell *et al.,* 2005), it is highly probable that both Severn and local Bann derived glass eel contribute to spawners.

Capture and transport

The condition (stress, damage etc) of glass eels for direct stocking will have a bearing on their eventual survival and growth, and may be more critical (and uncertain) than for fish held and on-grown in aquaculture facilities (where disease can be treated, and mortality levels measured). Thus, the methods used for collection may contribute to the level of production of silver eels. Obviously, capture and transfer methods should be used that maximize the survival of the transported eels and minimize stress, and the source fisheries should be selected with this in mind. It is not the purpose of this review to discuss capture and translocation methods and equipment, which will be well known to those who supply glass eels to aquaculturists, for example.

Although transport techniques and operations have developed considerably (and now include air freight) and survival rates are now considerably higher), the following extract is illustrative of potential problems with translocation. Bogdan and Waluga (1980) reported significant mortalities during transport of glass eels from France to Poland and in the days following. The glass eels were loaded into tanks of fresh or brackish water (4-8 ppt) at a density of between 75 and 105 kg m^{-3} and transported by road for 26 to 42 hours. Eight samples of glass eels, one each from two separate tanks in four shipments into Poland, were held (without feeding) for 18 days. Total losses ranged from 6.5 to 53%, with the higher levels of mortality being associated with poorer water quality in the transport tanks on arrival in Poland, particularly higher levels of ammoniacal nitrogen (12.5-47.4 mg/l vs 6.32-12.10 mg/l) and higher suspended solids (160-180 mg/l vs 3-5 mg/l). Bogdan and Waluga (1980) noted that the surviving elvers had increased susceptibility to unfavourable environmental conditions, which might also result in further losses, and the authors concluded that the method of long transport as used at that time should be considered to be arduous and unfavourable for elvers.

Though eels are a resilient species, being tolerant of low dissolved oxygen levels, changes in salinity and extreme temperatures, it is best to avoid large changes in environmental conditions during transport, and transfer during the hottest part of the day should be avoided in the summer months. Solomon and Aprahamian (2009) suggested that transit times should be minimised, that care should be taken to ensure that the water source at the donor site is appropriate for transfer, and that the transport containers used are capable of sustaining good water quality during the transfer, including more frequent exchanges of water if long distances are involved (which carry their own risks and problems).

It is clear that catching and transport practices have important implications for the survival and "fitness" of glass eels in particular and there are no welfare standards for commercial fisheries (P Woods pers. comm.). The European Food Safety Authority (EFSA) recommended that fishing for glass eels if they are used for aquaculture should be covered by aquaculture welfare regulations (EFSA, 2008), and this could equally apply to stocking.

Environment and habitat suitability for stocking

Though eels colonize marine, estuarine or freshwater habitats and are capable of making the transition between full seawater and freshwater (Kim *et al.,* 2006), there is a potential for stress when eels are transferred between seawater, brackish and freshwater environments. Glass eels are generally caught in the brackish waters of estuaries (e.g. Severn Estuary, UK) and even where salinity levels are high (below tidal barrages, e.g. Vilaine Estuary, France), and they could experience osmoregulatory stress when transferred directly to fresh water. However, Crean *et al.* (2005) observed 100% survival over 21 days when batches of glass eels and semi-pigmented elvers were transferred directly from estuary conditions into either fresh water, 50% sea water or full sea water, and glass eels have been transferred from fresh to full sea water in coastal rearing sites with no adverse reports (P. Woods pers. comm.). Solomon and Aprahamian (2009) suggest that transfer between waters of different salinities is not an issue in this context.

Behavioural differences have been observed between glass eels that appear to have elected to remain in saltwater and those destined to colonize freshwater habitats (Edeline *et al.,* 2005). Preference for freshwater was linked to high locomotor activity, a behaviour likely to facilitate dispersion through freshwater habitats in the wild, including into low density and lake habitats that support production of large female eels (Krueger and Oliveira 1999; Oliveira *et al.,* 2001). In contrast, low locomotor activity coupled to a preference for saltwater is likely to promote settlement in marine or estuarine habitats. Freshwater-contingent glass eels exhibited growth similar to those observed in native freshwater eel populations, whilst the saltwater-contingent glass eels had higher growth rates, as observed in native marine and estuarine populations (Tseng *et al.,* 2003; Arai *et al.,* 2004; Jessop *et al.,* 2004).

These results indicate that environmental salinity may directly affect juvenile eel growth and are in accordance with anecdotal information from eel culture which suggests that glass eels and elvers grow faster in saltwater than in freshwater. Growth rate is of major importance in terms of eventual silver eel production, and has been suggested to influence sexual differentiation and age and size at silvering in both sexes (Vøllestad 1992; Holmgren and Mosegaard 1996).

These observations could potentially complicate the choice with regards to sourcing glass eel for stocking. If the salinity preference revealed by Edeline *et al.,* (2005) persists when glass eels with low locomotor activity are transferred to freshwater, for example, do they continue to exhibit this trait or does the environment promote a change in activity to enhance migration? This risk could be reduced if glass eels or elvers that have already elected to move into low salinity environments are used for stocking, and/or stocking is carried out across target habitats rather than relying on dispersion from one location.

Williams and Aprahamian (2004) discussed the elements of habitat suitability for eels, and observed that there is little quantitative data on the eels' physical requirements, though the species appears very catholic in its choice of habitat. Yellow eels are found in all water types from coastal marine through brackish estuaries, in eutrophic and oligotrophic, shallow and deep still waters, and throughout rivers to their upland head waters. The main limiting factors appear to be barriers to migration and distance from the sea, and anthropogenic impacts on water quality. Williams and Aprahamian suggested that suitable habitat for stocking eel would be those where the eel density is low and likely to be less than the carrying capacity of the habitat, e.g. upstream of major obstructions to their migration and in the middle and upper reaches of catchments. Ideally, the sites should have a pH between 5 and 8 (Alabaster and Lloyd, 1982), a high degree of physical heterogeneity, both within the water course and riparian zone, and provide a high amount of cover and a diverse food supply. Knights *et al.,* (2001) suggested using sites with soft sediment, crevices and vegetation, since eels have negative phototaxis and benefit from adequate cover in the form of aquatic plants, undercut stream banks, bank vegetation and large woody debris.

Laffaille *et al.* (2005a) studied the processes governing the microhabitat distribution of European eel in a reclaimed freshwater marsh along the French Atlantic coast, and showed that eel densities were significantly related to the width of ditch section, the silt depth, and the density of emergent plants. Laffaille *et al.* (2005b) also demonstrated significant relationships between eel density and depth and water velocity in the River Frémur in NW France, noting that habitat preferences differed between size classes: large eels tended to be found in intermediate to deeper habitats with less aquatic vegetation, whereas smaller eels were mainly found in shallow habitats with an abundance of aquatic vegetation and were absent or rare in areas of deep water with a silty substrate.

WGEEL (ICES, 2003) developed a model with which a Habitat Suitability Index for life stage-specific components such as elver, yellow and silver eel can be calculated, with a score between 0 (not suitable for a viable population) and 1 (optimal habitat). However, this model used habitat data averaged over regions, countries and catchments, and this approach will only be of use to guide stocking site selection if appropriate habitat assessment data are available.

Growth of eels largely depends on temperature and food availability, for the latter of which intra- and inter-specific competition has to be taken into account. Optimum temperature for growth in eel is 20-26°C (Sadler, 1979; Tesch, 1983; Gousset, 1990), and growth ceases at temperatures below 10°C (Elie and Daguzan, 1976). Thus, both the average temperature during the growing season and the length of the growing season affect growth and the time taken to reach maturity, and the number of days when temperatures exceed 14°-16°C is often considered critical (Tesch, 1977; Deelder, 1984; Wickström *et al*, 1996) These are important considerations (in addition to knowing that the local eel population is depleted) when deciding where to stock. Obviously, the subsequent potential for exploitation and other sources of mortalities, e.g. intakes for turbines or abstraction, piscivores, etc must also take into account.
Eels need to be capable of dispering following stocking, and Symonds (2006) suggests that sites which promote congregation should ideally be avoided, both as donors or recipients

(though this is exactly the situation at some European collecting sites (e.g. below barrages). Several studies (Lannin and Liew 1979; Liew 1982; Feunteun *et al.,* 1998; Haro *et al.,* 2000) allude to similar effects for both American and European eels congregating in the area immediately downstream of a dam or other structure, where high densities could lead to increased predation, competition for food, or disease. High population density caused by structures that inhibit upstream movement may also lead to male predominance (see sex determination).

Williams and Aprahamian (2004) proposed that eels should be scatter stocked (to minimise density-dependent effects) in rivers during the summer, when temperatures are high enough to encourage dispersal, at densities of between 1 and 2 eels m^{-2} in low productivity waters, rising to 4-5 eels m^{-2} in warmer waters with plenty of bottom cover and/or marginal vegetation and high macro invertebrate productivity. Though they suggested stocking in a minimum 5-year rotation programme, this did not take into account the deficit of eel production in any specific catchment (in relation to EMPs).

The EU's ERP implies that enhancement of yellow eel populations and silver eel escapement in individual catchments contributes to achieving the management target set for the respective RBD. Stocking will therefore be most effective if aimed at those parts of catchments that will support high survival and growth rates, i.e. where eel densities are currently well below the carrying capacity of the habitat or its potential production, or can be shown to be depleted compared to historical or expected levels. It is implicit (though not explicit) that stocking through EMPs should be aimed solely at increasing the production of silver eels that will contribute to the spawning biomass, in waters with free access to the sea (or where effective downstream translocation can be otherwise arranged).

WGEEL (ICES, 2006) discussed the concept of a water body's carrying capacity (defined as the maximum density or biomass of a species that the habitat can sustain under average conditions) in relation to deciding where or whether to stock eel. For eels, however, carrying capacity is a difficult concept, given the plasticity of eel production dynamics in terms of numbers and biomass and with sex-related differences in growth and age/size at silvering. For example, a reach could produce high densities of eels that are mostly male and which migrate relatively early at low individual weights, so annual production of silver eels could be high in terms of biomass but relatively low in terms of spawning potential compared with a similar reach that produced fewer but larger females. Whether a site is at carrying capacity is also linked to ease of access for colonisation and the productivity of the water. In tributaries of the lower Severn, for example, Aprahamian (2000) found eel densities and biomass ranging over an order of magnitude (0.12-1.14 ind.m^{-2} and 2.56–25.24 g.m^{-2}, respectively) and there was no relationship between growth and either density or biomass, which suggests that these sites were close to or at their carrying capacity. Calculating carrying capacity of a river or lake for eel is not straightforward, nor is it easy to measure density and/or biomass of eel accurately in a given body of water (Williams and Aprahamian, 2004).

Although there are quantitative tools with which to establish whether a reach is at or approaching carrying capacity (Acou *et al.* 2011), for present purposes we are primarily concerned not with estimating carrying capacity *per se*, but whether the increased density of the combined native + stocked population can have a negative effect on growth and/or survival rates of the whole population or either component. In general, eel density declines with distance from the sea (Lobon-Cervia *et al.,* 1995; Knights *et al.*, 2001; Ibbotson *et al.*, 2002; Feunteun *et al.*, 2003), and sites more than 25-30 km above the tidal influence are likely to be below their carrying capacity for eel (Aprahamian, 1988; Feunteun, 2002). The reduction in eel density as one travels upriver is due in part to physical obstructions to upstream migration and distance (migration time) from the oceanic source of recruiting glass eels coupled with a reduction in the abundance of each recruiting cohort through time (mortality). Aprahamian *et al.* (2007) showed that, in England and Wales, there is a negative relationship between river gradient and eel density, in which steeper gradients reduce the distance of upstream migration of yellow eels and hence the production of silver eels. Thus, sites upstream of obstructions and in the upper reaches of rivers would be expected to have a low density of eel, making them potentially suitable areas for stocking. These effects are magnified when recruitment is low (as now), such that only the lower reaches of a catchment may have eel populations approaching “normal” densities. Knights (2005) suggests that the River Thames is a case in point.

WGEEL (ICES, 2008) suggest that greater attention should be given to local eel biomass when trying to assess whether a site is at carrying capacity, arguing that there is a smaller variation in biomass when compared to density both within and among river systems (Aprahamian, 1986) and biomass is more directly related to carrying capacity (Knights *et al.,*, 2001). Even though the ERP target (EU COM 1100/2007) is expressed in terms of silver eel biomass, stocking with elvers is aimed at restoring populations in the medium to long term (10-20 years, though earlier in the Mediterranean region), and population structure and the densities of eels < 15 cm are probably of more relevance to stocking than absolute biomass. Note, however, that we know almost nothing about the intra-specific and inter-specific factors that influence density-dependent effects in eels.

Berg and Jørgensen (1994) followed the fate of approximately 2 million eels, captured as glass eels from the Severn Estuary and grown on in warm water to 0.31-1.08 g, that were released in batches of between 1kg and 31 kg at 63 sites in eel-less branches of the River Gudenå in Denmark in 1987 and 1988, as part of a restoration programme. Eels were then recaptured by electric fishing between 46 and 146 days later. The key findings were that eels did not disperse far (<1 km), that scatter stocking resulted in better survival than focal stocking, and that average survival rates over 100 days, based on recapture rates, were low at 17.7% and 23.1% in 1987 and 1988 respectively.

It is worth mentioning here that densities of eel estimated from electric fishing surveys may be misleading and survival rates may be underestimates, since small eels are not effectively sampled by electric fishing (Aprahamian, 1986; Naismith and Knights, 1990a; Knights *et al.,*, 1996) and more widespread dispersal might be expected (White and Knights, 1997a,b; Knight *et al*, 2001). Surveys can only be conducted in daylight, when eels are hiding in burrows or crevices, and eels can be relatively difficult to see and capture, especially in dense submerged or emergent vegetation and in turbid waters >1 m deep. Catches, therefore, often increase on successive runs (Naismith and Knights 1990a; Knights, White and Naismith1996), which defeats the constant catchability assumption of multi-pass depletion analysis (Carle and Strub, 1978). As a consequence, eel densities and biomasses at many sites may be underestimated, though Knights *et al.* (2001) suggest that capture efficiencies can be increased up to four fold by using relatively high voltages and focusing on eels alone. Another complicating factor is that densities of eels can vary enormously between sites, even those very close together and, because eels may disperse at night to feed, the effective population density may be quite different from that observed when electric fishing. Furthermore, catch efficiencies are relatively low for smaller eels (<30cm) so the electric fishing may underestimate the actual density. These effects must be borne in mind when interpreting such data on eel abundance

Berg and Jørgensen (1994) concluded that the optimum density for scatter stocking was about 5-6 eels m^{-2}, similar to natural ranges for Danish streams soon after initial recruitment. These densities would be expected to decrease through time, and natural population densities found in other rivers are usually much lower, typically between 0.001 and 0.3 eels m^{-2}, 0.3-10 g m^{-2} (Tesch, 1977; Naismith and Knights, 1993; Knights *et al.,* 2001. These values are well below those of Williams and Aprahamian (2004), who suggested that a site is likely to be below carrying capacity for eel if the density is < 2 eels m^{-2} and < 2.5 g m^{-2}, or the site is greater than 30 km from the tidal influence.

Solomon and Aprahamian (2009) expressed some doubt about the validity of Berg and Jørgensen’s (1994) results, noting that the eels that were scatter stocked had a survival rate over 60-70 days of between 23.6% (stocking density 5.68/m^2) and 30.6% (0.62/m^2), a mortality rate between 7 and 16 times greater than that occurring naturally. They also noted that the fish used had an inconsistent history of rearing in captivity prior to release, and it is likely that the transport and rearing process had both reduced the viability of the stocked fish and contributed to impaired dispersion behaviour (see on-growing section).

Pragmatically, Solomon and Aprahamian (2009) suggest that it is reasonable to expect that stocking a water body in which eels are already present in good numbers will be less effective, or even lead to reduced production (density effects on growth and survival). For England and Wales, they propose that any reach of running water that is likely to already hold eels at a density lower than that to be stocked annually, viz 0.03 ind.m^{-2}, should not influence the survival of stocked elvers, neither would the level of stocking proposed affect survival and growth of the natural population.

ICES (2003) reports a study on density-dependent effects on migratory behaviour in a small river system (the Frémur, in NW France) based on methodology developed by Pollard *et al.* (1987). Annual densities by eel size class (<150 mm, 150-300, 300-450, >450 mm, of native origin) were measured for 6 years at 22 stations (Robinet *et al.,* 2008). There was a significant correlation between densities at adjacent stations for all size classes, and the relationship suggests that, in this river, density-dependent migration behaviour occurred at densities of 25 to 30 eels m^{-2}. Density-dependent effects appeared to be significant within size classes, but not between size classes, though this may have been an artefact of the differing migratory tendency between these size classes of eel (eels >300 mm are suggested to be relatively sedentary, Baras *et al*., 1998).

A follow up to this study looked for evidence for habitat limitations on eels (Acou *et al.,* 2011), using a General Linear Model to test simultaneously the effects of temporal, macro- and meso-scale habitat factors on the presence and absence of eels and their abundance at 30 sites over an 8-year period. Almost every site sampled had eels, whatever its location in the Frémur catchment, and eel densities were mainly influenced by the availability of suitable habitats (rocky substratum and in-stream cover). This suggests that the animals distribute themselves according to habitat suitability. Despite marked variability in natural recruitment to the Frémur, the density of the oldest size-class remained stable over 8 years, which Acou *et al*. (2011) suggested revealed density-dependent mortality due, probably, to intra-specific competition for space and food. From these observations, the authors suggested that eel habitats in the river Frémur are saturated, and that the mean density of eels observed (0.40 individuals m^{-2}), which is at the upper range of other values for European catchments, could serve as a threshold value for other male-dominated river stocks (provided they have a similar availability of suitable habitats).

A study by Lasne *et al.,* (2007) in the River Loire in France assumed that behaviour and habitat requirements change with eel size. They split their data set into the same four size classes as in the Frémur study above, and noted that densities were greatest in water bodies that have unimpeded connections to the river system. Density patterns were mostly influenced by small eels, which decreased upstream such that eels ≤150 mm were most abundant in the estuary and almost totally absent above the tidal limit, and eels 150-300 mm were almost absent from reaches >40 km above the tidal limit. Densities of eels >300 mm were always low and homogenous across the catchment.

In the absence of robust data on density thresholds for the eel's life history processes, Walker *et al.,* (2009) suggested that the densities or biomass of eel in reaches close to the estuary (<30 km), observed prior to the recruitment decline, indicate the population size at which density-dependence may have had an effect. Clearly, this is a topic that requires further investigation.

Ongrowing – is there a net benefit to survival or growth?

The practice of holding and on-growing glass eels in aquaculture facilities before release has been perceived to confer some advantage, both by allowing the fish to recover from stressful capture and transport practices (including transfer between different environments) and increasing overall survival rates. It also provides a quarantine opportunity, especially if international transport is involved. In her review of the potential to use stocking as an enhancement tool for American eel, Symonds (2006) noted that many difficulties have been found when rearing eels in captivity and the cost-benefit of using cultured juveniles must be assessed. Though facilities to hold and grow-on millions of elvers are likely to be expensive to create and operate, the success of aquaculture enterprises that use wild-origin glass eels in countries such as Sweden suggests that this may be less of a problem with European eels, and where a proportion of aquaculture production has often been used for stocking (albeit to support fisheries).

It has been argued that, because the contribution of stocked eels to the yellow eel population (and silver eel escapement) is governed largely by their survival and growth, the option to maximise both of these by on-growing glass eels/elvers before stocking may more than offset the extra costs of holding compared to immediate release. However, Klein Breteler (1994) concluded that culturing glass eels to juvenile size (presumably, small yellow eels) increases costs by 4-12 times compared to direct stocking with glass eels, and that the advantages in survival and growth rates were only marginal.

White and Knights' (1994) suggestion, that any initial growth advantage in the resulting yellow eels is lost after about 5-6 years, is supported by a study on five German lakes without natural eel recruitment that were stocked with both glass eels from England and farm-sourced eels every two years from 2004 to 2010 (Simon, poster to WFC 2012). Before stocking, the glass eels were chemically marked, and the farmed eels were individually tagged with a coded wire tag (cwt). The eel populations were monitored each year by electro-fishing and fyke nets, and a mark-recapture experiment was carried out in 2010. Eels stocked directly as glass eels showed a better growth and condition compared with eels stocked as farm eels, and had caught up in body size within three to four years after stocking. Survival rates of eels stocked as glass eels and as farmed eels after three to five years were similar. The authors suggest that the results demonstrate that the stocked farm eels had no advance in survival and growth compared with glass eels and that the stocking of usually more expensive farm eels may provide no general advantage compared with the stocking of glass eels.

Solomon and Aprahamian (2009) noted a Swedish programme that reared elvers in high density for ten weeks appeared to result in a preponderance of males in the stocked population, and Rossi *et al.,* (1988a) found that a group of the smallest cultured yellow eels after grading stocked in a lagoon system in Italy produced all male silver eels. Symonds (2006) also pointed out that cultured eels may be biased in favour of males due to high rearing densities experienced during culture conditions, suggesting that it is preferable to use eels for stocking that are sexually undifferentiated or with a higher percentage of females than males. Rearing eels at low density in captivity is probably not an option, given the high costs of on-growing, neither is the use of sex steroid treatment to manipulate sex (Colombo and Grandi 1990; Andersen *et al.,* 1996; Tzchori *et al.,* 2004), since released eels might eventually be harvested for human consumption.

Svasand (2004) pointed out that exposure to an artificial environment during on-growing can affect the phenotype and behaviour of reared individual eels and thus reduce their chances of survival, including weaning onto natural food after stocking (Rodriguez *et al.,* 2005). Symonds (2006) provides a summary of the possible causes of poor quality, and of the precautions that should be taken to prepare eels for a successful transition from the hatchery to the natural environment. These include the development of normal coloration and morphology, and normal feeding, migratory and anti-predator behaviour (reviewed by Brown and Laland, 2001). The rearing environment lacks natural behavioural cues and natural selection pressures, and predation on release can be high, caused by lack of acclimation and the stress caused by transportation, although the latter is also applicable to directly stocked eels. Symonds (2006) suggested that acclimation of cultured eels to natural conditions (e.g. temperature, photoperiod, flows etc), and using tanks with enriched environments can help condition fish for release (Masuda 2004), but these add to the culture costs. Other concerns surrounding holding elvers for on-growing is that this may increase rather than decrease the disease risk, though health management should be well practised in established aquaculture facilities.

There is some empirical evidence available to compare the quality of cultured and wild-caught stocked eels. For example, Bisgaard and Pedersen (1991) directly compared the performance in a Danish stream of native eels with scatter-stocked eel imported as glass eels from England and France and grown on in an eel farm in mid-Jutland, both groups being tagged with visible implant tags. After one year, recapture rates were 33.6 and 8.0% respectively and, whilst there was no significant difference in growth rate of the two groups of eels, the survival rate of native eels was estimated to be twice that of stocked cultured eels. However, nearly all the native eels were recaptured within the tagging site (it probably represented their “home” range), whilst cultured eels dispersed away from the stocking site, which could account for the apparent low survival rate of cultured eels as determined by mark-and-recapture.

Another comparison between stocked wild-caught and cultured eels was made by Pedersen (2000), who stocked native (in 1988) and cultured yellow eels (in 1989) into a man-made lake from which they could not escape. The total lake population was estimated by mark-recapture in 1996, when growth rates were found to be higher in the native eels and survival slightly better than cultured eels.

Rossi *et al.,* (1988a,b) compared the performance of natural residents with cultured yellow eels in a lagoon system in Italy, the cultured eels being allocated to two groups: one with good growth and a second being the smallest yellow eels after grading. Growth rates were similar between all groups of eels after 7 months, though the cultured eels exhibited lower survival rates than native eels and produced predominantly males silver eels.

The Dutch DUPAN foundation, which seeks to improve sustainable working practices of eel fisheries, eel farms and eel traders, is currently investigating whether eel farms can make an effective contribution to eel stock recovery. Glass eels can be reared in eel farms to become available for stocking as “fingerlings” at between 5 and 50 g, and DUPAN (2011) describes trials to compare the feeding behaviour and growth in glass eels and farm-reared fingerlings held in aquaria and fed natural food items, Daphnia, Tubifex and mosquito larvae. The glass eels responded to and finished the natural food within two hours, whilst the on-grown fingerlings were more tentative in approaching the food, remains of which were often found in the tank the next day. This difference in foraging behaviour was reflected in the respective batches’ growth: glass eels achieved an average increase of 2.34 % weight/day and 0.47 % length/day accompanied by an increase in condition factor (weight for length) from 0.073 to 0.114 after 47 days, whilst the farm-reared fingerlings gained only 0.06 % weight and 0.08 % length per day on average (the reference in eel farms is 1.35 %/day when fed artificial food), and their condition factor remained around 0.144.

DUPAN (2011) also investigated post-stocking growth and survival of glass eels and fingerlings reared on commercial feed, by stocking each of 3 pond sections with 100 glass eels and 3 pond sections with 100 fingerlings each. Carp *Cyprinus carpio* and tench *Tinca tinca* (which are unlikely to eat eels) that were ready to spawn were added in each pond section in order to bioturbate the sediments and to provide fish eggs and fry as an additional food source for the eels. Mark-recapture estimates indicated that 91 % of the glass eels and 97 % of the farm-reared fingerlings survived after 26 weeks, the glass eels growing from an average of 6.7 cm to 19.4 cm (2.17 % weight/day), whilst the fingerlings increased from an average of 18.4 to 23.9 cm (0.47 % weight/day).

DUPAN’s authors observed that the fingerlings displayed more social interactions than the glass eels in the rearing tanks, and suggest that this may account for their more limited growth when fed natural food items. They also consider that on-grown fingerlings tend to be more sensitive to rearing conditions in the ponds than glass eels. Nevertheless, the growth rates observed over the course of the experiment were similar to the average growth rates reported in the literature for native eel populations, and the survival rates of glass eels and farm-reared fingerlings in presence of natural food sources and absence of predation were similar at around 95 %. DUPAN's conclusion was that these results do not support the assumption that a higher yield can be obtained by rearing glass eels to fingerlings in farms prior to stocking, compared to stocking with glass eels.

Summary

Clearly, the efficacy of on-growing prior to stocking depends to a large extent on the subsequent survival and growth in the wild, compared to glass eels stocked directly. Although ICES (2007) considered that stocking with healthy on-grown eels will result in growth rates and mortalities comparable to stocking with glass eels (based on relatively few, mostly Scandinavian, studies: Vollestad and Johnson, 1988; Wickstrom *et al.,*, 1996; Moriarty and Dekker, 1997; Svedang, 1999), the evidence presented above suggests that there are few if any gains to be made from on-growing glass eels in situations where they can be stocked soon after capture from the wild. Solomon and Aprahamian (2009) note that the mortality rate of fish stocked after being grown-on for a matter of weeks before release was some ten times higher in the first few months than those occurring naturally (Berg and Jørgensen, 1994), suggesting that this might be expected to influence the behaviour and survival of the fish upon release, when they have to forage for natural food types quite different to those with which they have become familiar. They suggested that the most reliable approach may be to stock with glass eels as soon as possible after they have been captured (as does ICES, 2011). Clearly, stress and subsequent mortality following transportation are not necessarily less in aquaculture facilities than in the natural environment, and any gains in growth and/or survival during on-growing appear to be largely dissipated in part because the cultured eels have been conditioned to artificial environment and food opportunities and are less "fitted" for the wild. Note, however, that the availability of glass eels in Europe is greatest between December and March, when temperatures in Northern Europe are too low for direct stocking (lakes in the Baltic states the are still frozen), which implies that holding and on-growing in farms has a role if only to delay availability for stocking.

Post stocking survival to silver eel stage

A number of Swedish studies provide empirical evidence that eels stocked as glass eel, following a period in aquaculture, or as small yellow eels obtained from rivers on the west coast of Sweden survive, do grow and mature to the silver eel stage and start their outward migration (Wickström 1986b, Westin 1990, Wickström *et al.,* 1996, Pedersen 2000, Wickström 2001, Clevestam and Wickström 2008). Silver eels of stocked origin are caught in substantial quantities in lakes where no natural eel stock occurs. In lake Ången, for example, 17% of the stocked eels were recaptured as silver eel (860 eels) in an emigration trap (Wickström 1986a, 2001 and unpublished), whilst more than 7,000 silver eels (11.3 % of those stocked 14 years previously as elvers imported from the Bay of Biscay and grown on for 7 months and stocked at a mean weight of 2.9 g) had left Lake Fardume Träsk as descending yellow and silver eels by 2000 (Wickström 2001). In lake Götemaren, which is oligotrophic and has lower productivity and was stocked with 124 elvers.ha^{-1} which is 6 times the recommended stocking (25 elvers.ha^{-1} yr^{-1}), however, very few eels were caught in the traps, despite good recaptures in earlier surveys and similar pre-release culture conditions (Wickström *et al.,* 1996).

Williams and Aprahamian (2004) found little reliable information in the literature on mortality rates of stocked eel, even from long-term studies, because of unknown losses to migration and to unrecorded fishing mortality (Knights *et al*, 1996). Dekker (1999b) estimated that 75% of eel recruits die from natural causes, equivalent to an annual total mortality rate (Z) of 0.1-0.2 over a life span at 14-7 years respectively. Vøllestad and Johnsson (1988) studied natural recruitment to, and escapement from, the River Imsa in Norway between 1975 and 1987, and estimated Z to be 0.17. Similar Z values are quoted by Berg and Jørgensen (1994) from stocking the River Gudena with cultured juveniles, which appeared to have an initial high mortality over the one season of the study. Longer-term Z values for stocked eels appear to be much higher: 0.36-0.65 for a Danish stream (Rasmussen and Therkildsen, 1979), and 0.5-0.7 for the River Thames (Naismith and Knights, 1997), though, again, neither migration nor natural recruitment was accounted for in either of these studies.

Tesch (1999) suggested that the expected recapture rate from glass eel stocking would generally not be higher than 10%, based on a number of studies which he cited. Leopold (1976) recorded a loss of between 89% and 94.5% from glass eel stocking until catch in Polish waters with low natural recruitment, and the same order of magnitude was reported for Lake Constance (Hahlbeck and Kuhlmann, 1997). Kostyuchenko and Prishchepov (1972), working in Belarus reported a mean loss rate until recapture of 96% from an initial stocking with glass eels (23-300 ind.ha^{-1}), whilst Schäperclaus (1949) estimated loss rates from stocking with wild-caught young yellow eel (typical size around 30 g) until commercial catch to be about 40-60%, and losses from stocking with glass eel to be 80%.

Other relevant studies are Pedersen (2000), who estimated survival 7-8 years after stocking in Denmark to be 55-75% for wild-caught eels (19 g) and 42-57% for on-grown eels (40 g), whilst Knösche *et al.* (2004) estimated fishery recapture rates after stocking with glass eels at densities commonly used in German waters to range from 26% at 50.ha^{-1} decreasing to 4% at 500.ha^{-1}. Wickstrom (1993) estimated survival rates of 5-10% and upwards for elvers stocked in oligotrophic lakes at 25 ha^{-1}, and in eutrophic lakes at 100 ha^{-1}; and 40-80% for yellow eels stocked at 5 ha^{-1} in medium size oligotrophic lakes and 20 h^{-1} in eutrophic lakes.
There is limited information on the success of stocking marine waters using cultured eel. Andersson *et al.* (1991) reported a recapture rate of 3.5% within 7 years after stocking with elvers in open Swedish coastal waters. Pedersen (2010) describes a study in which 100,000 glass eels grown on for 3–6 month to around 3 or 9 g were tagged with coded wire tags (cwt) and released in the inner part of Roskilde Fjord (Denmark) during the summers of 1998 and 1999. The salinity of this shallow fjord ranges from 12 ppt where freshwater streams enter to 18 ppt where the fjord meets the Kattegat. Landings from fisheries in the fjord were checked for cwt-tagged eel, and recaptured eels were sexed and a small sample of otoliths was analysed for Sr/Ca content.

During the period 2000-2006, the overall recapture rate of the stocked fish (carrying cwt) was 1.8 %. Sr/Ca analysis indicated that they had not entered freshwater subsequent to stocking, and the numbers recaptured gradually decreased with distance from the stocking site (this is a common outcome of fish tagging studies). The annual growth increment of stocked eel was between 30 and 75 mm, and the sex ratio was 1:2 (M:F) in yellow eels but 50:1 (M:F) in silver eels, possibly as a result of higher fishing mortality on females during their longer residence in the Fjord before silvering. Though similar numbers of large (9 g) and small (3 g) eels were stocked, the proportions in recaptures were 39.7 % and 60.3 % respectively, which led Pedersen (2010) to suggest that the small eel was more valuable as stocking material than the larger eels. Pedersen estimated that stocking saline Roskilde Fjord with 3 g eel provides a possible catch to fishermen of at least 10.3 % of a stocked cohort (6.8% for eels, with another 5 % estimated to leave the fjord as silver eels (though total silver output without fishing would be less than the minimum estimated survival of 18%, due to natural mortality). Unfortunately, there are no corresponding values for glass eels stocked directly with which to make a direct comparison between stocked and native eels in this study (M. Pedersen, pers. comm.).

There are relatively few similar studies in the Mediterranean region. Desprez *et al,* (submitted) used a capture-recapture model employing demographic parameters of a stocked population of French eels to estimate population size and predict the number of silver eels obtained by stocking. They found that the stage at which eels were stocked did not influence their future survival and that the maximal number of silver eels was reached 4 years following stocking. Their conclusion was that stocking in the Mediterranean region is efficient for fast production of silver eels, though further studies are required to assess their quality (fitness for spawning) and sex ratios. Ciccotti (1997) reported a survival rate of 2% for eels stocked as glass eels and 34% for farmed eels (5g) in the Valle Nuova, Italy.

Solomon and Aprahamian (2009) reported two studies in which the relationship between numbers of elvers stocked and the resulting catches in yellow and silver eels in fisheries indicate how survival varies with stocking density in the same environment. Levels of stocking ranging from 20 to around 700 glass eel equivalent ha^{-1} yr^{-1} in Rangsdorfer See, Germany (ICES 2002), resulted in 5% to 30% of stocked fish being recaptured seven years after release, with the maximum level of recapture (presumably reflecting maximum level of survival) occurring at the lowest density stocked. A similar analysis for Lough Neagh, Northern Ireland (ICES 2007), indicated density-dependent mortality at anything above the lowest stocking rate of around 150 elvers ha^{-1} with survival rates through to the yellow eel and silver eel fisheries (the latter being very efficient) ranging from around 10% to over 40% at a stocking rate of 200/ha^{-}1, though this may be an over-estimate of true survival due to a contribution from natural recruitment.

Knösche *et al,* (2004) give a formula to estimate the recapture rate after stocking for a range of stocking densities common used for German waters (50-500 glass eel equivalents ha^{-1}).

Recapture rate (%) = 611 * stocking density $^{-0.81}$

At a stocking density of 50 glass eels.ha^{-1}, this would result in a recapture rate of 26%, whereas at 500 glass eels.ha^{-1} the recapture rate would decrease to 4% - and so reflects some density-dependence. Knösche *et al.* reported a mean recapture rate of 8.3 % (range 2-20%) for glass eel stocking from several literature studies, and 37.3 % (range 20-90%) from stocking with small wild-caught yellow eels.

It could be argued that the survival of elvers stocked at low densities in fresh water would be at least as good as those stocked at any higher level, and that there is no perceived risk of spreading the stock too thinly. The three examples above suggest that high levels of survival of elvers stocked into lakes can occur at low stocking densities, around 20 - 50 ind.ha^{-1} yr^{-1}, and that survival decreases exponentially with an increase in stocking density.

There is much less information on stocking rivers, where density levels are generally quoted in numbers m^{-2} (i.e. 10,000 x numbers ha^{-1}). Levels generally recommended for rivers are of the order of 3 to 5 elvers m^{-2} per year (Knights and White 1998, Williams and Aprahamian 2004), a hundred times higher than densities suggested for even shallow productive lakes. Solomon and Aprahamian (2009) postulate that the densities recommended for stocking in rivers are based upon the maximum observed densities of small eels in natural streams, which arise from many years of natural recruitment rather than one stocking experience, and that elvers stocked each year at such a level throughout a catchment would experience significant density-dependent mortality.

Solomon and Aprahamian (2009) suggest that, as the aim of any stocking programme would be to maximise the survival from elvers to adult (and not necessarily to maximise the eel production within the receiving water body), and that high survival rates from elver to adult (in excess of 25%) have been observed following stocking at low densities, the optimal approach is to stock at a low level over a wide area. As noted above, high survival of elvers stocked into productive lakes appears to occur at levels around 30 ind.ha^{-1}; whilst a reasonable starting point for rivers and streams might be ten times higher that of still waters. This suggests an annual stocking level for rivers and streams of 300. ha^{-1}, preferably in waters with no natural eels (as opposed to low natural stocks), in potentially productive areas such as lowland rivers of high trophic status and in geographical locations nearer rather than distant from the donor source, to minimise any residual concern over potential disruption of adult navigation.

Solomon and Aprahamian (2009) noted that reported annual levels of stocking in lakes have generally been between 20 to 500 glass eels (or glass-eel equivalents) per ha (0.002 to 0.05 per m^2). This is partly because the carrying capacity and productivity of large lakes may be less than that of rivers, and partly through recognition that there is likely to be a substantial population of older eels already present. Nevertheless, these relatively low stocking densities are associated with high survival rates to catchable size (probably yellow eels rather than silver eels), ranging from 5 to 30% or higher, depending upon the stocking density and the particular site. Overall, Solomon and Aprahamian (2009) suggest it is reasonable to assume a survival rate of the order of 25% for glass eels or elvers stocked into lakes at low densities, similar to the observed "lifetime" survival rate of 27% observed for native elvers entering a Norwegian river (Vøllestad and Jonsson, 1988).

It is extremely difficult to summarise the results of these studies in any quantitative way, as the methods used to estimate survival or mortality vary considerably, as do the conditions under which stocking and output were measured (site characteristics; source of stock; fishery/trap/sampling etc). Consequently, there are too many variables to present the results in tabular form without losing (or complicating) the essential information I have presented above. It can be concluded, nevertheless, that survival of stocked glass eels to either fishery-size yellow eels or silver eels falls within mainly the range 5-10% (exceptionally ~ 25%, depending on stocking density), whilst the corresponding value for stocked small yellow eels is 40-60%.

Growth

The numerous observations of the success of stocking as a means to increase fishery catches of mainly yellow eel (e.g. Moriarty and Dekker, 1997; White and Knights, 1997; Rosell *et al*., 2005; Psuty and Bohdan, 2008) suggests that stocked eels do survive and grow in a way comparable to natural immigrants and positively enhance the yield of the standing population, at least for fish stocked at younger ages. Lin *et al.* (2007) showed no differences in growth between stocked and natural eels in Lithuania, where natural eels are smaller than stocked eels of the same age, possibly due to energy loss while migrating the long way towards Lithuania.

Regular monitoring of wild eels for growth is difficult, but Pedersen (1999) estimated weight-at-age for farmed eel using a Von Bertalanffy growth equation to smooth growth from initial weight to final weight, showing that the intrinsic growth rate (% day^{-1}) was a function of eel size and time, declining with age from around 3% day^{-1} to 0.3% day^{-1} at an average weight of about 150 g after 18 months.
ICES (2006) reported the growth of native European eels to vary between 14 and 62 $mm.year^{-1}$ across the species' distribution range. This means that it will take 5-21 years for males to reach the average size of 37 cm at silvering, whilst female eels will take twice as long to reach 67 cm (see Maturation, below). For glass eels stocked in 2012, the effects on silver eel escapement could be expected from 2017 (at the earliest) to approximately 2050, depending partly on stocking location, sexual differentiation and growth. If the stocked eels are not hampered by anthropogenic factors, they could contribute to silver eel escapement after 10 years (and earlier in Mediterranean habitats).

Aprahamian (1986, 1987) reported that stocked eels grew approximately three-times faster than eels recruited naturally in the lower and middle reaches of the River Severn (UK), and Aprahamian (1988) observed that eels stocked in suitable habitats might, therefore, mature earlier than if left where they had recruited naturally. Verreault *et al.* (2010) also revealed a faster growth of stocked American eel, which matured at a length of 57 – 67 cm in the St Lawrence River compared to naturally migrating silver eel that are most generally > 80 cm in the St. Lawrence Estuary.

As might be expected, there are site-specific effects on growth, which is faster in salt water than in freshwater for both *A. anguilla* (e.g. Melia *et al.,* 2006a,b; Edeline *et al.,* 2005) and *A. rostrata* (Cote *et al.,* 2009). Wickström *et al.* (1996) and Clevestam and Wickström (2008) report substantial variation between Swedish lakes in size and weight of silver eels of stocked origin, and in their growth and age at silvering. Svedäng *et al.* (1996), Clevestam and Wickström (2008) and Lin *et al.* (2007) concluded that habitat differences and temperature determine growth rate, and that it is negatively correlated with age at silvering.

It is worth noting that any comparisons of growth (for example) between native and stocked eels need to take account of the possibility that the eels sampled may have spent much of their lives in a habitat with a different level of productivity to that in which they are caught. Tzeng (2009), for example, categorized sampled eels' life-history trajectories based on Sr/Ca ratios in the otoliths, which indicated a slower growth of stocked versus natural eels in three inland water bodies in Latvia. Wickström (2001) analysed the Sr/Ca ratio in the otoliths of yellow eels from two productive water bodies, Lake Ymsen and Lake Sörfjärden, to describe the length of time the eels spent in fresh, brackish or marine waters, i.e. were they recruited to the lakes as elvers or yellow eels (Sr/Ca content correlates with salinity: Arai et al., 2004). Both lakes had no natural recruitment and had been regularly stocked with both elvers and yellow eels. Growth rates were not found to be significantly different between fish stocked as elvers or yellow eels, and elvers appeared to have a lower mortality than fish stocked as yellow eels. Wickström (2001) stresses, however, that the quantity of data used in this study was limited.

Stocking density and yield per recruit

A simple mathematical method to evaluate the potential production from recruitment (in our case glass eels or elvers) to a particular life stage (in our case silver eel) is the conventional yield per recruit (Y/R) analysis. This requires estimates of the mean weight of the eel at each age and of natural mortality (and fishing mortality where exploitation occurs) by age/life stage, applied to a known number of recruits (or a nominal value, often 1000). Frost *et al.* (2001) used this approach to compare the economic benefits from different uses of glass eel, based on biological information about the life history stages from glass eel to silver eel derived from Dekker (1999b). A dynamic pool model (often referred to as a Beverton-Holt model) was used to describe the simultaneous development of several cohorts of glass eels recruited in consecutive years, with different parameter values to calculate annual catches in a "wild" fishery (including stocking) or eel-farm production. They estimated that stocking with 1 kg of glass eel per year provided additional annual catches of 96 kg, assuming that stocking is done continuously, that fishing on yellow eel commences when the eel is 6 years old (100 g), and that silvering starts when the eel is 10 years old at an average weight of 500 g. These estimates do not take into account the losses due to predation (i.e. natural mortality).

Walker *et al.* (2009) reviewed the available estimates of Y/R for eel, most of which are obtained from stocking in lakes. These range from 5 to 72 g recruit^{-1} (glass eel - mean weight of 0.3 g), though they are mainly in the range 20-50 g per stocked eel, i.e. 1 kg of stocked eel produces 60 – 150 kg yellow eels. For the purpose of estimating the total amount of glass eels used for stocking, yellow eel numbers were translated into glass eel numbers (glass eel equivalents) by correction factors usually used in Denmark (1 farmed eel equals 1.385 glass eels; M. I. Pedersen, pers. comm.) and Germany (1 farmed eel equals 3 glass eels; e. g. Knösche *et al.,* 2004).

The outcomes of individual studies on recruitment and yield are briefly presented below.

Finland

Some eight million glass eels/elvers and 700,000 small yellow eels (averaging 19.1 g, mainly from Sweden) were imported into Finland between 1960 and 1979. Pursiainen and Toivenen (1984) calculated Y/R at between 10 g and 90 g in northern and southern lakes respectively, with an average of 72 g. No specific stocking density or yield per unit area data were given, and the reliability of the effort and catch-return data is uncertain since non-professional fishermen made almost all the catches. Growth rates are slow in cold Finnish lakes compared with more southern waters, averaging 10-30 mm y^{-1} (Tulonen, 1990).

Sweden
The proportion of elvers used in a stocking programme in Sweden has slowly increased, despite the fishermen's traditional preference for stocking with small yellow eels. In 1999, 90 t of yellow eels from Skagerrak/Kattegat and 2.2 million imported elvers were stocked. Detailed monitoring of a shallow oligo/mesotrophic lake and another relatively deep and more oligotrophic lake commenced in 1980, using French-origin glass eels/elvers on-grown to 3-4 g and stocked at densities of 2.2 and 2.0 kg.ha^{-1} respectively (Wickström, 1986; Wickström *et al.,*1996). Fyke netting, long lining and outlet trapping in the shallow, more productive lake caught 11.4% of the stocked eels after 15 years, mainly as emigrant silver eels in traps, of which 70% were females. The annual yield averaged 1.24 kg.ha^{-1} between 1990 and 1994 (cumulative 13.3 g $recruit^{-1}$). Temperatures only exceed 14°C for about 4.5 months per year and were below 5°C for 6.5 months, and growth rates were slow, so it is likely that some female silver eels would emigrate after 15 years (the average age at silvering for stocked eel in Sweden is 14 years R. Fordham, pers comm).

A further stocking of elvers into the same Swedish lakes took place in 1989, but age determinations indicated that the bulk of silver eels caught up to 1995 originated from the first stocking. Wickström *et al.* (1996) suggested that competition with larger eels might have reduced the early growth rate of the second cohort.

Poland
Leopold and Bninska (1984) estimated that an average of 129 glass eels ha^{-1} yr^{-1} yielded 19 g $recruit^{-1}$, equivalent to 2.4 kg ha^{-1} in Polish lakes. They compared data from 454 lakes stocked with imported glass eels and elvers over 20-30 years. Stocking rates had risen to an average of over 100 eels ha^{-1} yr^{-1} by 1980. Commercial fishery yields varied from an average of 15.5 g $recruit^{-1}$ (equivalent to 2.8 kg ha^{-1}) from oligotrophic lakes to 22 g $recruit^{-1}$ (3.2 kg ha^{-1}) for smaller, shallower and more meso/eutrophic lakes with similar fishing effort. From another study of 86 Polish lakes, Moriarty *et al.* (1990) estimated optimum stocking density to be 275 glass eels ha^{-1} yielding 19 g $recruit^{-1}$ or 5.2 kg ha^{-1}, but without unrecorded losses due to escapement and recreational fishermen. Leopold and Bninska (1984) estimated that the latter's catch could have been 2.6 times the commercial yield, in which case yields might be as high as 85.5 g $recruit^{-1}$, or 4.6 kg ha^{-1}. These figures are similar to those for the eutrophic Great Mazurian Lake system, where a stocking rate of 62.7 glass eels/elvers ha^{-1} produced yields of up to 68.6 g $recruit^{-1}$, or 4.3 kg ha^{-1}. From a study on glass eel stocking in 559 Polish lakes, Tesch (1999) estimated that 21-40 glass eels / ha are needed for surplus yield of 1 kg ha^{-1} (25-48 g $recruit^{-1}$).

Germany
Early studies (cited by Tesch, 1999) include Strophal (1930), who observed that the yield in Lake Vilmsee, east Pomerania, increased from 0.7 to 3-8 kg ha^{-1} after stocking with wild-caught 15-30 cm yellow eels (av. 20 g) at a density of 14 ind. ha^{-1}, with a surplus yield of around 1 kg ha^{-1} indicating a recapture rate of about 40%. Gollub (1963) reported similar findings for Lake Röggliner See in Mecklenburg-Pomerania, where stocking of 30 small wild-caught yellow eels ha^{-1} led to a yield of 8 kg ha^{-1}, with surplus yield of 1 kg ha^{-1} derived from about 4 stocked eels ha^{-1}. Waters with low natural eel densities near Berlin stocked with glass eels at 750 ha^{-1} yielded up to 40 kg ha^{-1}, equivalent to a 53 g $recruit^{-1}$ (or 19 glass eels ha^{-1} needed for a yield of 1 kg ha^{-1}) (Albrecht, 1975). Hahlbeck and Kuhlmann (1997) reported glass eels stocked into Lake Constance to yield 3-6 kg ha^{-1}.

Ireland

In the 1970s, it was suggested that the annual yield from the Shannon catchment could be raised to 20-40 kg ha^{-1} by stocking at about 500 glass eels/elvers ha^{-1} each year (Quigley and O'Brien, 1993). However, though annual stocking rates of lakes between 1959 and 1991 averaged about 350 glass eels/elver ha^{-1}, which Moriarty (1982) suggested could yield 20 kg ha^{-1}, recorded annual yields of yellow and silver eels were in the order of 0.7 and 1.8 kg ha^{-1} respectively, equivalent to 2- 5 g $recruit^{-1}$. The authors suggested that these lower-than-predicted yields may have been due to relatively low fishing effort. Koops (1967, cited in Tesch 1999) reported relatively high yields in Lough Neagh, Northern Ireland, of around 20 kg ha^{-1} and suggested that 45 glass eels ha^{-1} are needed for a (surplus) yield of 1 kg ha^{-1}, representing 22 g $recruit^{-1}$.

Following a crash in natural recruitment to Lough Neagh in 1983, glass eels were imported from the Severn Estuary during 1984-1988, 1992, and 1994-2003. The stocking rate used was around 444 glass eels/elvers ha^{-1}, which yielded 16.1 kg ha^{-1} yellow eels and 5.5 kg ha^{-1} silver eels, equivalent to an average of 49 g $recruit^{-1}$ (Winfield *et al.,* 1993). More recent analysis based on tagging experiments to estimate silver eel escapement (Rosell *et al.,* 2005) suggests an annual silver eel production of around 2.5 to 3.5 kg. ha^{-1}.

Using a time-series analysis model relating stocking and catch in Lough Neagh, McCarthy and Blaszkowski (2006) suggested that yields were proportional to stocking at rates between 215 and 523 elvers ha^{-1}, up to a maximum of 26.3 kg ha^{-1}. There was evidence of increasing density-dependent effects on growth rates and survival at higher densities. McCarthy and Blaszkowski (2006) also estimated that the annual stocking rates required to achieve commercially viable yields ranged between 150 glass eels/elvers ha^{-1} in the less productive Corrib catchment to 450 ha^{-1} in the Shannon system. They postulated that high past stocking densities (400-450 ha^{-1}) may have led to a bias towards males in catches.

A more recent analysis of yellow and silver eel fishery yields from L. Neagh in relation to glass eel stocked (ICES, 2007) suggests a density-dependent relationship with a negative exponential between input stock and eventual output. Outputs in terms of catch or yellow and silver eels were maximal for inputs in the range of 150 to 200 glass eel ha^{-1}. Overall survival from stocking is estimated to be about 25% and the mean annual yield to the L. Neagh eel fishery is 49 g $recruit^{-1}$, assuming an average body weight of market-size yellow/ silver eels of 250 g.

England

Knights and White (1997) suggest that relatively low densities would help enhance the development of later maturing and larger females of high fecundity, and concluded that in warmer and more productive still waters, suitable densities would be about 0.1 kg ha^{-1} (i.e. about 300 glass eels/elvers ha^{-1}), giving a potential yield of ~20 kg ha^{-1}, or 40-50 g $recruit^{-1}$. They suggested that, in colder and less productive still waters, stocking rates should be reduced to 150-200 eels ha^{-1}.

Mediterranean

Natural recruitment to the brackish Commachio lagoons in Italy has been supplemented in the past with 15-20 cm yellow eels caught in French lagoons, as well as some on-grown glass eels (Rossi *et al.,*1988b). The lower average body size in catches compared with fish from more northern European waters is compensated for by higher productivity and yields of smaller yellow eels, e.g. 58-113 g $recruit^{-1}$ or 29 kg ha^{-1}.

A number of studies have attempted to provide more generalised information on stocking and yield values for European eel. Moriarty and Dekker (1997) noted that stocking rates of glass eel which varied between 0.1 and 0.5 kg ha^{-1} (300 – 1500 ha^{-1}) could be assumed to provide 10 kg ha^{-1} of yellow and silver eel in freshwater systems, around 20 kg ha^{-1} in saline closed systems (e.g. lagoons) and some 5 kg ha^{-1} in open saline systems, such as the Baltic Sea. The lower values may reflect the loss of potential yield due to emigration away from fisheries. These authors suggest that, in warm, highly productive still waters, a 40-50 g $recruit^{-1}$is typical.

Tesch (1999) estimated that, under favourable conditions, about 15 glass eels or 5 small yellow eels will produce a yield increase of 1 kg ha^{-1} (ca. 67 g $recruit^{-1}$), whilst WGEEL (ICES 2001) gives 20-90 g $recruit^{-1}$ (glass eel) for the Baltic region.
Table 1 below summarises the results of studies on Y/R from stocked eels. Note that Y/R for stocked yellow eels are not directly comparable with those for glass eels unless back calculated to glass eel stage. There is obviously a confounding effect of stocking density and potential productivity of the water body into which eels are stocked, but it is apparent that yields within the range 20-70 g $recruit^{-1}$ (4-14 kg ha^{-1}, at a stocking density of 200 glass eels ha^{-1}) might be expected. The higher yields (kg ha^{-1}) quoted for some of the above studies may be associated more with potential fishery yield than eventual silver eel escapement.

Table 1. Yield per recruit estimates reported for specific European studies.

Location	**Water body**	**Age group stocked**	**Stocking density**	**Yield g $recruit^{-1}$**	**Reference**
Finland	Lakes	Glass eel and yellow eel (average 19.1g)		72 g (range 10-90 g)	Pursiainen and Toivenen (1984)
Poland	Lake	Glass eel	21-40 ha^{-1} yr^{-1}	25-48 g	Tesch (1999)
Poland	Lake	Glass eel	129 ha^{-1} yr^{-1}	19 g	Leopold (1976)
Poland	Lake	Glass eel	100 ha^{-1} yr^{-1}	15.5 -22.0 g	Leoplod and Bninska (1984)
Poland	Great Mazurian Lake system	Glass eel	62.7 ha^{-1} yr^{-1}	68.6 g	Leoplod and Bninska (1984)

Poland	Lake	Glass eel	275 ha^{-1} yr^{-1}	19 g (85.5g if include recreational catch)	Moriarty *et al.,* (1990) (Leoplod and Bninska (1984)
Sweden	Lake	Yellow eel (3-4 g)	600 ha^{-1}	13.3 g	Wickström *et al.,* (1996)
Germany	Lake	Glass eel	750 ha^{-1}	53 g	Albrecht (1975
N. Ireland	Lough Neagh	Glass eel	45 ha^{-1}	22 g	Koops (1967, cited in Tesch, 1999)
N. Ireland	Lough Neagh	Glass eel	444 ha^{-1}	49 g $recruit^{-1}$	Winfield *et al.,* (1993)
N. Ireland	Lough Neagh	Glass eel	150-200 ha^{-1}	49 g	ICES (2007)
Ireland	Lakes – Shannon system	Glass eel	350 ha^{-1}	2-5 g	Moriarty (1987)
UK (England and Wales)	Rivers	Glass eels	300 ha $^{-1}$	40-50 g	Knights & White (1997)
Italy	Lagoon	Yellow eel (150 – 200 mm)		58-113 g	Rossi *et al.* (1988a)

Sex differentiation

The foregoing has largely ignored the profound influence that the proportion of male and female eels (sex ratio) in a population will have on the age and size at which individual eels mature and hence the potential production of spawners. The physiological mechanism by which individual eels elect to become male or female is not well understood, and there is a scarcity of relevant information in the literature (reviewed by Davey and Jellyman, 2005). Grandi and Colombo (1997) and Grandi *et al*. (2003) histologically classified European eels as “undifferentiated” gonochorists, which means that final sex differentiation occurs from a juvenile hermaphroditic stage of a gonad with the general histological features of an early testis, but containing female and male primordial germ cells, oocytes and spermatogonia. This gonad later differentiates into a testis or an ovary. Male eels only acquire true testes once they reach the silver eel phase, while ovaries can be found in juvenile yellow eels. Beullens *et al.* (1997) also found that the undifferentiated gonad of the European eel can develop directly into an ovary, whereas differentiation of male sex proceeded via an inter-sex stage with male and female cells. It appears, therefore, that gonads differentiate into testes or ovaries during the growth phase of the yellow eels, and that an inter-sex period may occur which Andersen *et al*. (1996) suggests may represent an obligatory transitory phase or a facultative sex reversal stage induced by environmental conditions.

Sexual differentiation in eels appears to be quite plastic and may be influenced by density and growth rates (which are inter-related, see Davey and Jellyman, 2005). Many studies have suggested that conditions of high eel density favour a male-biased sex ratio. However, there are a number of factors that make it difficult to understand this process, or to derive the data required to describe and model the effects of density on ‘choice’ of sex (Walker *et al.,* 2009). Though we are not concerned here with sex ratio or density estimates for a whole catchment, since stocking is likely to be more local, linking sex ratio to density information is still not straightforward. Eels may spend 10 or more years in a river or lake, and are likely to differentiate during the first few years, so there might be a gap of several years between the time and place when the eels differentiated and that when density is calculated. Furthermore, male and female silver eels migrate at different ages, so the conditions that resulted in some eels becoming male might have been different from those that resulted in other eels becoming female, and the ratio measured across the observed length range may be biased towards females if males have already begun to silver and leave the site. Walker *et al.,* (2009) suggest, therefore, that sex ratio should be calculated for eels shorter than the length of the smallest male silver eel (30-35 cm).

Reviewing some French, Spanish and Norwegian studies, Robinet *et al.* (2008) suggest some relationships between whole-river eel density and sex-ratio of emigrating silver eels: rivers with densities > 500-1000 eels.ha^{-1} or 90-170 kg.ha^{-1} produce mainly male silver eels (>90%); whereas rivers with densities < 300 eels.ha^{-1} or 45 kg.ha^{-1} produce mostly female silver eels (>80%). This suggests a density threshold of around 500 eels.ha^{-1} around which the sex ratio of silver eels swaps from being dominated by one to the other sex.

Aprahamian (1988) showed that the sex ratio of yellow eels varied with the sampled part of the Rivers Severn and Dee (UK). The sex ratios for the whole of each river was around 42:58 (M:F), whilst densities observed in the River Severn ranged from 500 eels.ha^{-1} (in the upper catchment) to 32,000 eels.ha^{-1} (max. value in the lower catchment: information on eel density in the River Dee is not provided). These values are much higher than those indicated by Robinet *et al.* (2008) as the density limit that would produce mainly male silver eels. Although the two results are not directly comparable, they do provide some information about the range of density values that can be associated with a considerable proportion of females in the population.

Naismith and Knights (1990b) give M:F ratios for eels of length 30-32 cm that range from 1:9 to 12:1, depending on the part of the of the River Thames sampled, and also suggest that high M:F ratios are associated with high densities. However, the results are rather inconsistent, for example showing a M:F ratio of 11:3 for eels in a site with a “high” density, while this ratio is 18:3 in another site with a lower density. The sex ratio for eels <35 cm appears to be male dominated everywhere in the Thames, except in the outer more saline reaches, though it is not clear what proportion of eels at each length range in this study are classified as undifferentiated.

Bark *et al*. (2007) reported a significant relationship between whole-river densities (biomass; averaged across survey sites) and proportion of females for 5774 individual eels from a total of 128 sites across 8 catchments in England and Wales: % F = -32ln(density.100m^{-2}) + 138.5. Note that site biomass is not necessarily the same as density in numbers, which is likely to have more effect on sex ratio.

Walker *et al*. (2009) analysed data for 13 UK eel populations and found that the minimum length of sex-differentiated eels ranged from 15 to 21 cm, the minimum length of females ranged from 17 – 30 cm, whilst no males were found above about 38-41 cm. They noted that differentiation could last for several years in a single year-class cohort, but were unable to find information about the factors that could influence the length or age at which an eel becomes differentiated or the time it takes for all eels from a single cohort to differentiate.

Rosell *et al.* (2005) links an increase in the proportion of females in the silver eels caught recently in Lough Neagh to the relative lower elver numbers there since 1989. Based on estimates of elver densities in the (previous) period that were associated with high male proportions in silver eels, this indicated that annual recruitment of 75–100 g ha^{-1} will produce more males than females, with female output being the norm at < 50 g ha^{-1}. Although there are gaps in the information on sex ratio of silver eels between 1980 and 2000 and of elvers entering Lough Neagh between 1947 and 1960, Rosell *et al.* suggest that small changes in elver densities could lead to a change in the sex ratio of silver eels.

Clearly, information about the process of sex differentiation in eels in the wild is fragmented and sometimes contradictory, and some scientists have tried to study it in a controlled environment. Roncarati *et al.* (1997), for example, kept three groups of elvers in tanks at densities of approximately 1780, 3650 and 7200 eel.m^{-3}, which resulted in male to female ratios of 2:1, 3.5:1 and 25:1 respectively. Although these densities are much higher than those observed naturally, the proportion of females produced is considerable even at densities of 1780 and 3650 eels.m^{-3}. Note, however, that these eels were kept under much more favourable conditions that might be encountered in the wild (no shortage of food, constant temperature, etc.), which is reflected in the sizes the eels attained in 15 months (~52 cm for females and 42 cm for males). They do suggest, however, that under favourable conditions a high proportion of females could be produced at higher densities than in the wild.

For American eel, Symonds (2006) illustrated the influence of source material on sex determination by reference to Vladykov and Liew (1982), who reared elvers collected from two different populations, the Digdeguash River (New Brunswick) and the Grand-Riviere Blanche (Quebec), to the adult stage in similar conditions in the same freshwater pond in Ontario, 3 years apart. The New Brunswick sample was some 9000 partially-pigmented elvers (46 to 67 mm, mean weight 0.13 g) translocated in 1967, whilst approximately 7000 elvers (54 to 66 mm, mean weight 0.22 g) from Quebec were translocated in 1970. The sex ratios and growth rates of the two populations were different, with 71.2% males in the NB population and 27.2 % males in the Quebec population. Symonds (2006) commented that it is not clear whether local variations in conditions within the pond or genetic differences between the donor populations were sufficient to influence the growth rates and sex ratios, but cautioned that, if female silver eels are the preferred outcome from stocking, selection of donor and recipient sites should bear in mind that sex determination in eels is complex and poorly understood and, although influenced by environment, can be difficult to predict or control.

We might conclude, nevertheless, that stocking which changes the local density of eels may have an impact upon the sex ratio of the resulting population. Females seem to predominate in lower-density populations, and males in higher density populations, suggesting that sex is determined by the density of the stock and possibly by the growth opportunities afforded. Though the role of genetics and environmental conditions in sex determination are not clear, it appears likely that stocking of glass eels and elvers at low density, into areas with zero or low natural recruitment, will probably result in the majority of the adult output to be female. However, we do not know what we are aiming at. The cautious approach would be to stock at levels that bring local populations to “natural” densities and produce sex ratios close to what would be expected under historic natural conditions, if these are known.

The contribution of stocked eel (and natural recruits) to spawning success once European eels reach the Sargasso Sea will depend to some (but an unknown) extent on the sex ratio of the silver eels produced. Since sex differentiation in eel is unlikely to take place before the fully pigmented young eel stage, and at a body length of >15 cm, actual or potential sex ratios in most stocked eel are unknown. Wickström *et al.* (1996) pointed out that, where pre-grown eels from either aquaculture farms or natural water bodies have been stocked, the sex of at least a proportion of the stocking material might have been fixed before stocking. Observed sex ratios in eel populations at such sites after stocking would not be suitable to judge the effect of stocking on sex ratios.

Because there is strong evidence that sex ratio is density driven, there is a risk that removing glass eel from estuaries will affect subsequent gender differentiation and sex ratio of yellow eel and silver eel in the donor catchment. Similarly, translocating undifferentiated eels from high to relatively low density habitats may well influence ultimate sex ratio of the silver eel output, and by association, the weight and distribution of escapement through time. From this perspective, it is worth noting that the glass eel fishery in the Severn Estuary does not appear to have had any measurable negative impact on stocks of eel in the lower and middle reaches of the Severn catchment (Environment Agency, unpublished).

Maturation

Production in relation to recruitment or stock density of fish populations is conventionally expressed in terms of the biomass gain over all ages (i.e. a function of each recruiting cohort's growth and natural mortality) and as yield to fisheries by cohort or age group. An indication of a stock's reproductive potential is often expressed as spawning stock biomass, which is the standing stock of all extant cohorts weighted by the proportion of each age group that is sexually mature (often both sexes combined). In calculating eel production in relation to spawning escapement, therefore, we must take into account the age and size at which male and female yellow eels begin the process of maturation (silvering) and emigrate from the freshwater (and coastal) growing environment.

Silvering is a gradual process that appears to be initiated by a peak of growth hormone at the end of spring (Rohr *et al*., 2001). The urge to emigrate appears to be triggered by a drop in temperature in autumn, when the eels will stop feeding and begin a downstream migration under appropriate environmental conditions. In long continental rivers, it is quite probable that eels may travel to reach the sea over more than one year.

Pedersen (1999) reported that native male and female silver eels in Denmark had mean weights of 98 and 829 g respectively, whilst Frost *et al.* (2001) assumed that silvering starts at average weights of 100 g and 500 g respectively, based on Danish eel data provided by Pedersen. ICES (2006) reported that male eels have an average size of 37 cm at silvering, whilst female eels averaged 67 cm. Tesch (1977), in reviewing published data on this topic from different rivers in Europe, found silver male eels at 35-45 cm and females >45 cm (mean between 55 and 60 cm).

Aprahamian (1988) suggested that male eels leave the River Severn system at lengths ranging from 29 to 44 cm, while females migrate at 35 to 81 cm. The age frequency distribution for male silver eels ranged from 4 to 20 years (mode at 11-15 years), and for females 9-27 years (mode 13-22 years).

Naismith and Knights (1990) suggest that male eels in the River Thames silvered mainly between 33 and 40 cm at about 4 - 8 years (mode 5 years) and that the majority emigrated before attaining 41-45 cm. Females silvered at between 36 and 60 cm (8-11 years), and very few emigrated < 46 cm.

By way of comparison, high average temperatures and abundant natural productivity in the Mediterranean region encourage higher densities and fast growth in the Commachio lagoons in Italy, favouring the production of males, which matured on average at 2.5 years of age and comprised 80-90% of catches; females matured at around 3.6 years (Rossi, 1979). Lobon-Cervia et al. (1995) reported a population in Cantabria, Spain, which produces almost only males, at age 3-4. However, some lagoons, such as the Valle Nuova (Ferrara), can yield up to 90% females, maturing at 2-5 years of age (Rossi and Colombo, 1976).

It is apparent from the above examples that there is considerable variation in the size and age at which eels mature, though silvered male are usually smaller and emigrate at younger ages than females in the same catchment. The most obvious feature is that females can become mature and emigrate as silver eels after only 2-5 years in warm, productive habitats around the Mediterranean, whilst this process may take upwards of 30 years in cold Scandinavian waters.

Reproductive potential

Growth, as described above, has been defined in terms of length and/or weight gain, though studies on fat and energy content of European eel derived from coastal waters in the North Sea and Baltic Sea as well as from freshwaters in that region, and of body condition of various life stages of native and stocked American eel (Symonds 2006) are relevant to an evaluation of stocking success.

Silver European eels needs to migrate a minimum of 4000 km to reach the Sargasso Sea (McCleave*,* 1993) and must expend considerable energy to cover this large distance (van Ginneken *et al.,* 2005). This suggests that energy reserves, in the form of lipid, may be critical for successful migration to the spawning grounds, and Larsson *et al.* (1990) suggested that lipid levels may be the trigger for the decision to migrate, although this may not be a straightforward case of cause and effect (Svedäng and Wickström, 1997). Limburg *et al.* (2003) reported that silver eels caught exiting the Baltic Sea had a higher fat content (21.1% of body weight) than those collected in the Southern Baltic near Denmark (18.6%), but differences were not significant between native and presumed stocked fish within geographic areas.

Clevestam and Wickström (2008) showed that silver eels captured at Kullen and in Køge Bugt that were thought to be of fresh-water origin were younger, smaller and had higher fat content than stocked-origin silver eels from the Swedish fresh water lakes. They also suggest that eels with a catadromous life-strategy (assumed natural recruitment) are better equipped for migration and spawning than stocked eels (coastal or in fresh water), since the former are older, bigger, fatter and exhibit a higher degree of maturity when caught migrating out of the Baltic Sea. However, this may be an effect of the higher age (age is correlated with length) resulting from a catadromous strategy, (Svedäng *et al.,* 1996, Lin *et al.,* 2007). Clevestam and Wickström (2008) also showed that silver eels of stocked origin, coming from fresh water environments, show lower silvering indices (gonadosomatic, stomach, intestine, eye, and fin) than emigrating native eels in the Baltic outlet. There are, however, indications that silver eel leaving fresh water are less mature than those in the Baltic outlet, which is in line with other studies showing the gradual transition from yellow to silver stage (Durif *et al.,* 2005).

Although they have indicated that presumed native-origin silver eels tend to have better reproductive attributes that those of stocked origin, Clevestam and Wickström (2008) considered that the choice of stocking material (glass eel or small yellow eel) does not influence growth, age at silvering or silvering index, though the combination of chosen stocking material and the characteristics of the local habitats might have an effect. There are indications in Lake Roxen, for example, that glass eels grow faster, attain a lower fat content, lower age and GSI than stocked small yellow eels.

It has been suggested that potential spawning success may be evaluated by comparing the occurrence of oocyte atresia (indicating loss of potential eggs and recruits) between native and stocked silver eels as measured at various distances along their migration route. However, examination of such reproductive factors is not likely to reveal anything of use in the context of this review, as the complement of oocytes in all fish ovaries are “fine tuned” at some stage to balance the available energy reserves with the need to maximise egg quality at spawning time. This is one reason why early-term “fecundity”, such as measured when examining silver eels emigrating from rivers, does not allow us to predict the outcome in terms of recruitment per spawner (male and female) or, indeed, explain any stock-recruitment relationship.

Size and lipid content may also have an impact on the eels’ swimming energetics during oceanic migration. Clevestam *et al.* (2011) estimated that silver eels below a certain length will consume so much energy (derived from lipid stores) during their migration to the Sargasso Sea that they may not be capable of spawning successfully upon arrival, and that about 20% of silver eels leaving the Baltic Sea will arrive with a zero net lipid content (which is contra-intuitive, if we would expect that evolutionary drivers would be tuned to reproductive success). Nevertheless, individual eels produced in the northern part of the species' geographic range may contribute more to the populations' reproductive potential because average female size and female percentage appear to increase with latitude (Barbin and McCleave 1997, for the American eel). However, both American (Helfman *et al.,* 1987) and European eels grow more slowly and mature later in more northerly regions, so the contribution of maturing silver eels to reproductive potential will be much delayed compared to the equivalent recruitment further south. That is, stocking will have a slower impact on enhancing reproductive potential the further north one goes.

The contribution of stocked eels to the spawning run

There are a number of empirical examples of the success of stocking in terms of silver eel production. Large quantities (75 t) of silver eel were caught annually in an emigration trap at Siofok on the south side of Lake Balaton, Hungary, where only stocked eels occur (Bíró 1992, 1997). Ciepielewski (1976), Moriarty *et al.* (1990) and Robak (2005) report catches of emigrating eels originating from stocking in the Masurian marshes in north eastern Poland. Also, Järvalt (2009) reported large catches of silver eels from Lake Võrtsjärv in central Estonia as a result of large-scale stocking initiated after the power plant in Narva blocked all immigration to Lakes Peipsi and Võrtsjärv. A good example of how translocated eels (mainly from around the Mediterranean) become silver eels is demonstrated by long-established extensive eel farming in the lagoons at the Italian Comacchio, which are caught when they emigrate to the Adriatic Sea (De Leo and Gatto 2001).

Our knowledge of survival, growth, size and age at silvering of eels stocked and living in coastal marine environments is more uncertain than for populations in freshwater, in part because of the difficulty in identifying the habitats previously occupied by eels. Studies using otolith chemistry (Sr/Ca ratio) to indicate the origin and growing environment of emigrating silver eels coming out of the Baltic Sea have shown the presence of stocked eels. Limburg *et al.* (2003) used indices of maturity status and Sr/Ca ratio to establish the origin of silver eels collected at the exit of the Baltic Sea. Of 86 silver eels analyzed, 17 (20%) eels had Sr/Ca profiles consistent with having been stocked into fresh water, six (7%) showed patterns consistent with stocking directly into the Baltic from marine waters, and 10 showed patterns indicative of natural catadromy (i.e. migration into fresh water for growth). In all, 31.4% of silver eels showed histories of freshwater experience, including 24% of those found outside the Baltic, and the proportion of silver eels of stocked origin was higher among eels caught south of Lolland (Denmark) than among eels caught at Kullen (Sweden).

In a similar (Sr/Ca) study of emigrating eels caught at Kullen and Køge, Sweden, Clevestam and Wickström (2008) estimated the proportion of stocked eels to be 21%; about 10% stocked on the coast as elvers or small yellow eels and about 11% stocked into fresh water. Only 4.5% were classified as stocked and grown up in fresh water. Though a large proportion of the silver eels (70%) were not classifiable as to their recruitment background, the authors suggest that at least 12% are of stocked origin, consisting of both glass eels and small yellow eels with significant freshwater growth and eels stocked into fresh water that went more or less directly into coastal waters, all with very distinct Sr/Ca patterns. The group of eels whose origin was uncertain appeared to have experienced significant growth in brackish waters. Clevestam and Wickström (2008) also showed that the commercial catch of eels migrating from lakes located relatively far inland in Sweden, and with some barriers to immigration, is almost completely dominated by stocked eels.

Wickström *et al.* (2010) suggest that mortality due to migration obstacles, turbines and fishing may explain why the proportion of silver eels originating from fresh water is so low, and note that eels caught in southern Sweden may come from the east of the Baltic Sea.

Despite the evidence presented above, WGEEL (ICES, 2011b) has advised that no firm conclusions can be drawn as to quantifying the contribution of stocked eels to spawning escapement. However, a rough estimate based on stocking figures and subsequent silver eel run in the Baltic indicated that the observed percentage of silver eels from stocking origin is in reasonable agreement with expectation, and the parallel development of stocking and escapement also indicates that the fitness of stocked and naturally-recruited eels is similar. This conclusion is based on the estimate by Wickström *et al.,* (2010) that the observed proportion of stocked eels in the silver escapement from the Baltic Sea is 20-40%, which is roughly proportionate to the number of eels (glass eel and small yellow eel combined) stocked in the Baltic between 1990 and 2000, assuming a survival rate of 10% and individual weight of 0.8 kg per silver eel, and an estimate of the commercial catch of silver eel in the Baltic (data from ICES 2009). They indicate that some 65-90% of the silver eel run escapes the fishery, noting that the percentage of silver eels caught peaked in the 1960s at an average of 48% (Sjöberg *et al.,* 2008) and, with the current escapement level of about 30%, the expected contribution to the silver eel production from stocked origin will be within the range 8-40%. They caution, however, that this does not provide guidance how well stocked eels contribute to spawner escapement compared with natural immigrants (i.e. spawner quality, see above).

Behaviour of stocked vs native eels

Upstream dispersion

We have already discussed the possibility of behavioural differences between glass eels that appear to have elected to remain in saltwater and those destined to colonize freshwater habitats (Edeline *et al.,* 2005): the former exhibit low locomotor activity which is likely to promote settlement in marine or estuarine habitats; the latter being linked to high locomotor activity that which would facilitate dispersion, reduce local densities and, presumably, promote the production of large female eels (Krueger and Oliveira 1999; Oliveira *et al.,* 2001. Once in fresh water, however, it is thought that upstream migration of elvers and yellow eels is mainly driven by intra-specific competition and higher densities downstream, which would explain the general tendency for population densities to decrease with distance from tidal limits (Knights *et al.,* 2001, Aprahamian *et al.*, 2007). In addition to the direct effects on the size of the local population, therefore, a reduction in natural recruitment and hence density may lead to a reduction of dispersal of juvenile eel to habitats upstream of the donor site, resulting in lower densities further into the catchment. Ibbotson *et al.,* (2002) suggested that upstream migration of eels in the River Severn was mainly through diffusion, and that removal of stock from downstream areas may reduce the propensity for colonization of upstream areas. This effect is illustrated by an example from the River Vilaine (West France), where the construction of an estuarine dam prevented recruitment of eels for 25 years. On the installation of an eel pass, density-dependent migration behaviour was observed in which the periphery of the high-density area (about 0.8 eels m^{-2}) extended further upstream in successive years (Feunteun, 2002).

During migration from the open sea to estuarine and fresh waters, glass eels are highly sensitive to a number of chemicals, in particular vegetable odours (Tosi et al., 1990; Tosi and Sola 1993; Sola 1995; Sola and Tongiorgi 1996), which could be involved in con-specific recognition and may play a role in guiding the eels toward the coast. Various studies have revealed that L-amino acids may act as a cue for eels in both grouping and the search for food (Mackie and Mitchell 1983; Carrieri *et al.,* 1986; Sola and Tongiorgi 1998). Many of these substances have been shown to elicit a response in the eel at extremely low concentrations, and could play a fundamental orientating role in the upstream migration of glass eels. It is a moot point whether translocation of eels interferes with the potential for such stimuli's to promote movement and feeding within a recipient site and to enhance survival.

Emigration - from fresh water to sea

A question of prime relevance to the potential for stocked eels to contribute to spawning success and future recruitment in the native population is: do stocked and naturally recruited eels display the same ability to emigrate from the freshwater (or brackish/marine) growing habitat and migrate through the coastal zone and across the continental shelf towards the deep-water spawning ground? There have been suggestions (based mainly on anecdote and opinion, rather than hard evidence, it appears) that eels derived from stocking are less likely to contribute to the spawning stock due to lower fitness and, especially if they are shipped a considerable distance for release, due to a lack of navigational knowledge. A number of mark and recapture studies provide some useful evidence.

Since 2006, around 10% of almost 900 eels of varying size and sexual maturity and considered to be of stocked origin, tagged upstream of hydroelectric power plants in Narva, Estonia, were recaptured, mostly in the lakes where they were marked (which is to be expected) (Järvalt *et al.,* 2010). The few recaptures (7) reported outside the immediate vicinity of the tagging area, however, were all made towards the outlet to the Baltic Sea.

Westin (2003a) reported a tagging experiment in Sweden involving silver eels obtained from a trap in the outlet stream 500 m downstream of the lake where they had been stocked at about 3g, having been grown-on from glass eels imported from France. After tagging, the silver eels were released back into the lake or in the stream just above the trap. Those recaptured had lost weight and condition, and Westin hypothesised that the stocked eels had had no opportunity to imprint to the directional clues necessary for migration and lacked the orientation mechanism necessary to locate the outlet to the Baltic Sea. However, the fact that they were caught in the trap in the first place suggests that they were able to locate the lake's outlet and that subsequent behaviour is possibly related to capture and tagging. In contrast, Limburg *et al.*'s (2003) examination of the Sr/Ca content of the otoliths of silver eels caught at various points in the Baltic Sea (see above) found that 27% had probably originated from stocking. On the basis of these results, Solomon and Aprahamian (2009) concluded that there is little evidence either way as to whether transporting glass eels over a significant distance, and to rivers draining to different marine waters, interferes with their navigational ability as adults.

More recent work by Pedersen (2010) found that tagged silver eels of stocked (farmed) and native origin, captured during autumn and released in the inner part of Roskilde Fjord (which has a long and complex connection to the Kattegat) in autumn 2004 and 2005, resulted in a higher recapture rate of native eels (28%) compared to stocked eels (19%), though the difference is not statistically significant. Independent of origin, both eel types were caught in the same proportions in the southern and northern parts of the fjord (56% and 44% respectively), indicating similar migration patterns of the stocked and native silver eels towards the outlet of the fjord. Pedersen (2010) also found that previously stocked eel in a Danish brackish water lagoon started to emigrate as silver eel alongside those arising from natural immigrants (identified by otolith Sr/Ca ratios).

A similar observation was made by Verreault *et al.* (2010) for female American eels *A. rostrata,* caught in the brackish waters of the St. Lawrence Estuary and identified by fluorescent oxytetracycline marks on the otoliths as coming from glass eels caught in Nova Scotia and stocked four years earlier in the Richelieu River, 500 km upstream from the recapture location. The six silver eels of stocked origin had a very rapid growth and migrated out of the St Lawrence system in autumn at 4–6 years of age, compared to their native counterparts, 20–25 years, though they had gonads at a similar maturity stage. The authors suggest that these results provide evidence that American eels stocked as glass eels can migrate seaward at least as far as the estuary in synchrony with naturally recruited female silver eels en route to their spawning grounds in the Sargasso Sea.

It is not always so clear cut. In the Vistula lagoon on Poland's Baltic coast, there are indications that silver eels, probably of stocked origin, do not move towards the outlet in the northern part of the lagoon, but initially migrate westward where there is no connection to the sea (Wilkońska and Psuty, 2008).

Westin (1990, 1998, 2003a,b) carried out experiments with approximately 1800 marked silver eels, comparing eels from known origin (glass eel from France, stocked in Fardume

Träsk on Gotland) and unknown origin (silver eels caught in the Stockholm archipelago and on the coast of Gotland). The average recapture rate was 16% (9% for those of stocking origin and 20% for those with unknown origin), which is lower than other tagging studies in the Baltic Sea (Sjöberg and Petersson 2005). Though the tagging and release methods in the 14 experiments were not consistent, the author considered that because recaptures were made in the south-western Baltic Sea and there was a high degree of overwintering, the results showed that eels of stocked origin lack the necessary experience / imprinting from natural immigration to find their way out of the Baltic Sea.

In a review of 42 silver eel tagging experiments during the 20th century (approximately 7000 marked eels), Sjöberg and Peterson (2005) noted that fewer eels were caught in the Sound (Öresund) in the early 1970s than in the other exits from the Baltic. They suggest that a change in emigration pattern may be a result of extensive stocking, though note that many factors may be governing the choice of exits from the Baltic Sea. Subsequently, Sjöberg *et al.* (2008) carried out a statistical analysis of a much larger body of historical data, based on about 300 experiments between 1903 and 2006 in which 40,000 silver eels were tagged. The recapture rate averaged about 33%, and did not show any effect that can be related to the extensive stocking programmes in the Baltic region, given historical changes such as fluctuating fishing pressure which precludes an unambiguous analysis. Chemical analysis of a sample of recaptured tagged silver eels indicated that the majority (90%) had grown up in brackish water only. Sjöberg *et al.* (2008) suggest that the results show a well-functioning navigation ability in the recaptured migrating silver eels, which came from the natural environments around the Baltic Sea and would presumably consist of both natural migrants and ones of stocked origin.

Sjöberg and Wickström (2008) noted that recaptures of silver eels tagged in Lake Mälaren, most of which were of stocked origin, were made mainly within the lake itself, west of the release site, and show overwintering behaviour. The few eels caught outside the lake appeared to be migrating in the direction of the Baltic outlet, whilst other eels migrated west and then turned back and found the outlet to the Baltic (, unpublished.). Wickström *et al.* (2010) suggest that it is too early to say whether overwintering of putative silver eels in lakes is a natural behaviour or an effect that can be connected to stocking. The Lake Mälaren study is being continued and Sjöberg *et al*. (WFC, 2012) report that the eels have difficulties to find the outlets in the eastern part of the lake and continued to be caught in the lake 1-3 years after tagging, with significant weight losses.

DSTs will indicate whether westward migrating eels have overwintered and whether these eels were stocked or natural. Overwintering in rivers has been observed in native silver eels, but it is not known what causes this behaviour (Feunteun *et al.* 2000).

In light of these contrasting observations, and paying particular attention to the work of Westin in the 1990s, ICES (2011a) re-iterates its doubt about the ability of stocked eels to navigate properly during the migration. Clearly, a more detailed examination of the evidence is required, paying particular attention to the source and translocation history of stocked eels, though this is difficult to discern once eels have been released into the wild and only caught many years later as emigrating silver eel. The recent practice in Sweden of marking the otoliths of all stocked eels should provide the basis of such studies in the future.

It is not the remit of this review to evaluate the evidence for sensory mechanisms used in migration, though there is a possibility that imprinting (of odours, magnetic fields or other landmarks, as hypothesised for salmon: e.g. Hasler and Wisby, 1951; Taylor, 1986) by eels in earlier, immigrating life stages as they move through coastal and freshwater growing areas later informs navigation during the spawning migration. Durif (2012) comments that “Were that the case, there would be a possibility of disorientation leading to reduced emigration success as a result of translocation, but this has yet to be demonstrated either way”.

Orientation and navigation in European eel has been studied by many researchers (e.g. Hanson *et al.,* 1984; Hanson and Westerberg 1987, Tesch *et al.,* 1992: Westerberg and Begout-Anras 2000; Durif and Skiftesvik 2007). Nishi and Kawamura (2005), working with A. *japonica*, found that glass eels are sensitive to magnetic fields, and suggest that they may acquire and "memorize" geomagnetic information which silver eels use to find their way back to the oceanic spawning ground. However, if migrating silver eels do use the same cues and routes as the leptocephali, they may only have to reach coastal waters, since stocked eels have already traversed the open ocean and continental shelf and coastal waters before being caught as glass eels or elvers. Without specific knowledge on the sensory capabilities of eels, and how these are used to navigate, it is fruitless to speculate whether there are any such differences between stocked and natural eels that might explain migration behaviour.

Migration – at sea

Though the question of whether silver eels emigrating from freshwater (or coastal) habitats in Europe actually do spawn in the Sargasso Sea is crucial to any assessment of the contribution of stocked eels to the population's sustainability, this is outside the remit of this report. The key assumption in the EC's ERP is that an increase in the production of silver eels escaping to the sea results in an equivalent production of recruiting glass eels, tempered by any stock/recruitment relationship and by climate and environmental influences (as in any fish stock/population). The question of most immediate relevance is; do stocked and naturally recruited eels display the same ability to emigrate from the freshwater (or brackish/marine) growing habitat and migrate across through the coastal zone and across the continental shelf towards the deep-water spawning ground?

This is a minor objective of the EELIAD project (www.eeliad.com/project), within which a number of studies are being carried out through collaborating research projects, utilising a variety of developing scientific techniques such as tracking with satellite transmitters and data storage tags (DSTs), genetic analysis and advanced mathematical models. The ambitious overall objective is to find out what happens during the oceanic phase of the eel's spawning migration to the Sargasso Sea, and return larval route to Europe, i.e. to provide an overall picture of the eel's life cycle. Tagging experiments began in autumn 2008, but much of this work has yet to be formally presented or published. However, a brief account of some of the more relevant findings is proved below.

Westerberg and Sjöberg (2011) investigated behavioural differences between silver eels taken from the Enningdal River that were probably naturally recruited (native), and eels taken from the River Ätran above more than ten dams without eel ladders, which were most likely stocked as glass eel imported from the River Severn (UK). Fifteen eels in each group were tagged internally with coded acoustic transmitters and DSTs and a further 10 in each group with external DSTs. All 50 tagged eels were released at the head of a fjord on the Swedish west coast, in which receivers were moored across three transects to monitor the acoustic transmitters during the subsequent migration to the open sea. Though the absolute number of eels passing the different transects is not known, no statistically significant difference was found between the stocked and native eels in the time taken to reach the innermost transect and in the mean migration speed between subsequent transects. For both groups, swimming speeds reached velocities of approximately 40 km/day and individual eels covered the distance between transects in the fjord during a single night. Though the number of native eels observed leaving the fjord was 30% larger than the stocked group, the actual number of escaping eels is not known. One eel with a DST recovered at Lofoten was not detected at the mouth of the fjord.

Two DSTs with a reasonably long record of active migration have so far been recovered, one from an eel that was probably naturally immigrated (native) and one from an eel stocked as glass eel. They show a similar diurnal depth cycle - deep in daytime and shallower during the night – and both followed the Norwegian trench at an average depth >200 m, moving at about 30 km/day, a behaviour consistent with that found from DST-tagged silver eels leaving the Baltic. Westerberg and Sjöberg (2011) concluded that these experiments show no evidence of a difference in migration behaviour between stocked and naturally recruited eels.

A update of this work (Westerberg, Sjöberg and Økland, WFC, 2012) reports that a total of 80 silver eels with buoyant, implanted DSTs and 40 externally attached DSTs with programmable release were released at the west Swedish coast and in the Sound connecting the Baltic with Kattegat in 2008, 2009 and 2010. By autumn 2011, 20 % of the external tags and 2.5 % of the implanted tags have been recovered, five of which gave records of active migration from approximately 20 to 90 days. The migration route of all the eels was along the Norwegian Trench into the Norwegian Sea at 62-63° N and then southwest into the Atlantic west of Scotland. They observed that the migration route and the diurnal diving behaviour is representative for a normal silver eel migration as inferred from independent data on the temporal and spatial occurrence of migrating eels in scientific bottom trawl surveys. The abstract did not comment on the eels' origin.

Preliminary results from satellite tags (Aarestrup *et al.,* 2009) show that eels migrate at great depth and that the route from Swedish waters appears to be north of the British Isles. One eel, from Skåne, southern Sweden and of unknown origin, was shown to migrate to the north of the Shetlands. An unpublished update of this work reported the movements of tagged native and stocked silver eels after leaving the Norwegian west coast, passing between the Faroe and the Shetland islands to enter the Atlantic Ocean and were then tracked west of Britain before disappearing (due to predation, tag failure?). Although only a few eels were followed into the Atlantic, the conclusion by the Swedish participants was that, for as long as they could follow the migrating eels, there was no difference in behaviour between naturally recruited eels and stocked eels.

A follow up of the EELIAD experiment with stocked and naturally recruited eels was planned for autumn 2011, using both Microwave Telemetry satellite tags and internal programmable data storage tags to increase the return of data from the oceanic phase of the migration. More data is expected to accumulate over the coming months to explore the ability of native and stocked eels to navigate back to the Sargasso Sea.

Disease and parasites - risks to native stock

There is a possibility that diseases or parasites associated with translocated eels might pose a risk to native eels, and Williams and Threader (2007) addressed the risk of disease transfer when stocking eel. Symonds (2006) described several parasites, viruses, bacteria and fungi that have been found in eel communities in North America, whilst studies in Europe indicate that stocking and transfers have been responsible for spreading eel parasites and diseases (Szekely 1994; Van Ginneken *et al.,* 2004; EELREP 2005).

Probably the most well-know example is the nematode *Anguillicoloides crassus*, which causes damage to the swim bladder of the eel, including thickening of the swim bladder walls, a blocked pneumatic duct and rupture (Kirk, 2003). Palstra *et al.* (2007) suggest that the pathology inflicted on the swim bladder by this parasite and associated physiological effects may impair the capacity of European eels to undertake the migration to spawning grounds in the area of the Sargasso Sea. In trials in a large flume, Westerberg *et al.* (2007) and Sjöberg *et al.* (2009) showed that eels with a low infection in the swim bladder are more successful in swimming long distances and are more capable of carrying out vertical movements (than those with heavy infection), which Scaion *et al.* (2009) suggest are required to satisfy different physiological requirements during the long spawning migration. Though around 90% of all eels from Upper Lake Constance examined by Bernies *et al.* (2011) displayed swim bladder lesions, the growth and survival of infected yellow eels were not noticeably altered. However, the authors observed heavy swim bladder lesions in around 10% of silver eels, which they suggested would probably impair migration potential and thus the subsequent breeding success of the oceanic phase (though there does not appear to be any information that would allow one to compare stocked and native origin fish in this respect).

Infection with *A. crassus* has caused mortalities in farmed populations in the presence of other stressors (Kirk, 2003), and Van Banning and Haenen (1990) report that the nematode has caused serious losses in intensive eel production linked with secondary bacterial infections. Reports of parasite-induced host-mortality in native populations are less numerous and are all associated with adverse environmental stressors. Van Banning and Haenen (1990) noted that it is very difficult to compare losses primarily due to *A. crassus* in farmed and native eels because it is easier to detect dead or diseased eels in cultured.

As to the role of stocking in the spread of *A. crassus*, it is thought that the parasite was accidentally introduced into Europe in the early 1980s, possibly with importation of infected Japanese eels from Taiwan into northern Germany (Koops and Hartmann 1989; Køie 1991) where it was first detected in 1982 (Neumann 1985). The parasite then rapidly spread through the farmed and native eel populations in Europe, almost certainly facilitated by intra- and inter-catchment movement of eels for restocking and human consumption, though it is also thought that natural movements of eels in fresh, brackish and coastal waters have accelerated dissemination and extended its range. Though the sea was thought to act as a barrier to dissemination (Van Banning and Haenen 1990), Kirk *et al.* (2002) demonstrated that the parasite can survive and complete its life cycle in both marine and brackish waters, although infection levels are lower than in fresh water. Eels from sea water are usually free of *A. crassus*.

The only known limitations to dissemination of *A. crassus* appear to be availability of intermediate hosts (Kirk *et al.,* 2000b) and low temperatures (<4°C) (Hoglund *et al.,* 1992; Thomas and Ollevier 1993; Knopf *et al.,* 1998). However, the parasite has a relatively simple life cycle and is adaptable to a wide range of common intermediate hosts (Kennedy and Fitch 1990; Szekely 1994), coupled with free living stages that are capable of surviving and remaining viable in a range of environmental conditions (Kirk *et al.,* 2000b). Audenaer *et al.* (2003) observed that the prevalence of *A. crassus* in Flanders, Belgium, increased from 34.1% in 1987 to 68.7% by 2000, which they ascribed to stocking with glass eel and yellow eel. Ruffe *Gymnocephalus cernuus* and sunfish *Lepomis gibbosus* were implicated as hosts for *A. crassus* by Bernies *et al.* (2011) in Upper Lake Constance, where *A. crassus* was first recorded in eels in 1989 and prevalence reached 60% between 1992 and 2007. The rapid spread of the *A. crassus* throughout Europe indicates that eel transfer or stocking done without screening can put the eel population at risk of uinfection, though eels stocked from farms that use best quality glass eels and filters and quarantine should be free of the parasite.

Other parasites that have caused serious problems among captive European eels include the monogene *Pseudodactylogyrus anguillae* (Buchmann 1988; Buchmann *et al.,* 1987) which can result, ultimately, in respiratory failure (Chan and Wu 1984), whilst *Ergasilus sieboldi* and other *Ergasilus* spp. (Grabda 1991; Tuuha *et al.,* 1992) have caused causing haemorrhaging and gill inflammation, blockage of lamellar blood vessels and excessive production of gill mucus, again leading to both respiratory and osmoregulatory failure (Hogans 1989). Secondary infections of the fungus, *Saprolegnia* sp., have been also reported with *Ergasilus* spp. infections (Reichenbach-Klinke and Landolt 1973).

As with all diseases, losses and sub-lethal effects may be more intense (and more obvious, without treatment) in aquaculture situations, though stress due to translocation may also contribute to the impacts. A number of viruses have been isolated from European eels, among which the rhabdoviruses eel virus European-X (EVEX) and *Herpesvirus anguillae* HVA have received most attention (Jørgensen *et al.,*, 1994; van Nieuwstadt *et al.,* 2001; van Ginneken *et al.,* 2004). There have been documented losses to HVA in aquaculture (Lehmann *et al.,* 2005) as well as in the wild (Scheinert and Baath, 2004), and deliberate infection with HVA is reported as a practice to avoid uncontrolled disease outbreaks in aquaculture, including also the on-growing of glass eel for subsequent stocking. Proven negative impacts caused by EVEX-virus are rare (van Ginneken *et al.,* 2005), though infected European eels suffered from haematocrit decrease related to distance during simulated migration in large flumes, developed haemorrhage and anaemia, and died after 1000–1500 km "migration". Diseases caused by bacteria within eel culture were reviewed and described by Nielsen and Esteve-Gassent (2006), who considered the most important to be those caused by *Vibrio vulnificus* serovar E (formerly biotype 2) (Fouz *et al.,* 2006) and *Vibrio* (*Listonella*) *anguillarum*.

ICES (2011) concluded that, though the impacts on the native stock of the anthropogenic spread of viral diseases via stocking are unknown, they should be avoided, but did not say how to do this (presumably by screening and quarantine, as necessary). As culture techniques have improved, these diseases have become less of a problem, though no aquaculture rearing system is ever sterile. The aquaculturist can reduce the risk of disease by holding imported eels in quarantine facilities prior to transfer to the main culture system. Clearly, adherence to good biosecurity practices, development of health screening and disease management plans, water filtering and equipment disinfection and optimized rearing conditions can help maintain a healthy eel population. Screening of eels for parasites, viruses and pathogens takes place in England and Wales, and in some Swedish aquaculture sites, but not in France where the largest part of the European glass eel catch is taken. Clearly, using glass eels for stocking reducees the risk of introducing parasites. We should bear in mind, however, that the presence of pathogens in all species is a natural phenomenon, which is more likely to be a problem in intensively managed situations than in wild populations.

Genetic implications of stocking

There is a strongly held presumption that, where a diversity of genetic traits is apparent in a fish species, translocation of stock between areas should be avoided in order to preserve the inherent "fitness" of local populations. On this basis, there has been concern that there may be genetic risks associated with transfer and stocking of eels. Studies by Daemen *et al.* (2001), Wirth and Bernatchez (2001) and Maes and Volckaert (2002) found evidence for a weak but significant population structure in European eels, identifying three broad groups: Mediterranean, North Sea and Baltic, and northern (Iceland). Wirth and Bernatchez (2001) postulated that these could result from differences in migration pathways and distances to the Sargasso Sea, and some form of mating separation, and Kettle and Haines (2006) suggest that they may be explained by ocean currents resulting in a differential distribution of eel larvae (which presupposes some genetic variation at source). On this basis, ICES has previously (ICES 2007) recommended that eels should not be trans-located between river basins for stocking purposes or, if seen as indispensable to avoid an imminent collapse of specific river stocks, any stocking should be done within geographically proximate areas e.g. within the Mediterranean basin, the North Sea region, or the Baltic Sea.

These genetic variations have, however, proved to be unstable over time and, reviewing genetic studies of the European eel using allozyme and mitochondrial DNA markers, Dannewitz *et al.* (2005) could find no evidence of spatial genetic variation in samples of European eels. They concluded that eels sampled along the coasts of Europe and Africa most probably belong to a single spatially-homogeneous, genetic population, which is to be expected if silver eels aggregate in one location to spawn within a limited period in the Sargasso Sea, and the resulting glass eels do not necessarily "home" to the area in which their parents grew up.

Maes *et al.* (2006a) showed that the variance in genetic composition was low but significant between recruitment waves of glass eels within and between years, and suggested that this may be due to a broad-scale effect of spawning cohorts (i.e. adult reproductive contribution) and a smaller-scale variance in reproductive success among seasonally separated spawning groups, most likely originating from fluctuating oceanic and climatic forces (see Wirth and Bernatchez, 2001 above). The latter effect was indicated by Pujolar *et al.* (2006), who found highly significant genetic differentiation among eleven different arrival waves of glass eels collected at Den Oever, The Netherlands, in 2001 - 2003.

The current hypothesis is that all European eel comprise a single, randomly mating "panmictic" population (Palm *et al.*, 2009) and Als *et al.* (2011), using samples of early-stage eel larvae from the spawning area in the Sargasso Sea and of glass eel caught along the North African and European coasts between Morocco and North Cape, suggested that there is a random arrival of adult eels in the spawning area and subsequent random distribution of recruits to the coast.

Although Mank and Avise (2003) showed statistically significant population-genetic differentiation in American eel *A. rostrata*, they concluded that any departures from apparent eel panmixia are modest at best. Symonds (2006) suggests that the results to date imply that the American eel must be managed as a single panmictic population, and that conservation can be addressed effectively only on a global scale. Recent work by Bernatchez *et al.* (2011) has supported the hypothesis of panmixia for American eel.

On this basis, WGEEL (ICES 2009) concluded that there is no genetic argument against translocation of eels within its distribution area. Precautions must be taken, nevertheless, to ensure that the genetic integrity of the European eel is not compromised by stocking with aquaculture-grown eels that may contain *A. rostrata* (they have been found in Germany, Trautner *et al.,* 2006). When *A. anguilla* was in short supply and at a very high price, *A. rostrata* glass eels have been used in European aquaculture, but they are now much more expensive and have proved to be an unsatisfactory species to farm in Europe (P. Woods pers. comm.) At this stage it is difficult to distinguish macroscopically between the American and European eel, though Trautner et al. (2006) published a polymerase chain reaction (PCR) technique that provides a cost-effective method to discriminate between European and American eels.

We might conclude, therefore, that the imperative to enhance spawning success and recruitment across the whole European eel population probably outweighs any possible detrimental genetic effects that might result from stocking. Nevertheless, WGEEL (ICES, 2008) suggest that it is important to preserve the total genetic diversity to allow adaptation to a changing environment, and that keeping the highest level of biodiversity in phenotypic and genetic traits is crucial for the survival of the species. In this respect, work by Pujolar *et al.* (2011) on the effective population size of the European eel found no evidence for a genetic bottleneck, with moderate to high levels of genetic diversity. The authors suggest that the observed demographic decline in the European eel has not been accompanied by a genetic decline of the same magnitude. They also noted that a stable effective (genetic) population size suggests that the decline in eel recruitment has not been due to a reduction in spawning stock abundance, though it is impossible to evaluate the balance between maintenance of genetic diversity/integrity and the need to maximise spawner escapement from a severely depleted supply of recruits.

Other risks associated with stocking

WGEEL (ICES, 2008) identified the risks attached to stocking with glass eel, young yellow eels and on-grown eel from aquaculture, noting that diseases, parasites, biased sex-ratios and genetic selection may best be avoided by stocking with eels that are as young as possible. Stocking with yellow eel caught in the wild carries the risk of their being contaminated with pollutants such as PCBs, flame retardants, pesticides, heavy metals and endocrine disruptors, which some authors have suggested may potentially limit migration of silver eels to the spawning grounds and impair reproductive success (Larsson *et al.,* 1990; Robinet and Feunteun 2002; Palstra *et al.,* 2006). This applies equally to native eels left *in situ*, of course. WGEEL suggested that priority should, therefore, be given to sourcing stock from those sites where such contaminants are at the lowest possible levels, and pointed out that information on such areas is available through the European Eel Quality Database (see Chapter 6 of ICES, 2008). If on-grown eels from aquaculture are used, the main risks are spread of disease, reduced fitness for life in natural environments, and skewed sex ratios. Given these concerns, and the absence of evidence, WGEEL (2008) recommended stocking in high quality upstream habitats with glass eels from the same river's estuary or from neighbouring river basins or, where there is no recruitment, from the same main hydrographical region.

In this context, there appears to have been not formal risk assessment carried out for stocking with eels, which should attempt to balance any potential detrimental effects (disease or parasite transmission, genetic disruption, chemical contamination, behavioural traits and skewed population dynamics, of native and cultured stock fish) against the benefits of stocking in relation to the objectives of the EC's ERP.

Determining net benefit of stocking

Some of the reviews already discussed outline frameworks to assess eel stock status, identify habitat and biodiversity characteristics conducive to eel production and potential risks associated with stocking, and show how stocking programmes can be planned and their success or failure evaluated. They do not, however, provide a quantitative tool with which to compare stocking with other stock-enhancement approaches, or to guide the practicalities of an effective stocking programme within an EMP. Development of an EMP will require assessments of the status of the eel population within a river basin and an evaluation of whether or not stocking is an appropriate option to meet the management target.

It is not within the remit of this review to describe or evaluate the various mathematical models that can be used to provide quantitative estimates or predictions of the outcome of eel stocking, most of which are theoretical rather than based on empirical results, and it is emphasised that without validation these models do not provide evidence for or against the effectiveness of stocking as an option to aid recovery of the European eel. Nevertheless, it may help readers to understand the population dynamics of eels and the various implicated factors by briefly (and as critically as possible) describing two of the most recently developed models, selected to highlight the information and evidence that may be of use in the context of measuring the success of stocking. Much of what follows has a clear resonance with the previous findings of this review.

Walker *et al.* (2009) describe an Eel Stocking Assessment Tool (ESAT) that was developed in order to support decision making when stocking eel in river basins with the aim of increasing spawning escapement of silver eel from England and Wales towards EMP targets. The ESAT model incorporates eel production processes of growth, mortality, sex differentiation and maturation applied from the glass eel/elver to silver eel stages, based on existing models and those being developed.

Walker *et al.* (2009) assumed that the main ecological and practical aspects of planning and implementing a stocking programme have already been addressed (for the catchment in question) within the development of EMPs. That is, it has been demonstrated (by an estimate of silver eel escapement, or equivalent values for yellow eels as a surrogate for silver eels) that a catchment is not meeting its management target (a minimum of 40% escapement of silver eel biomass leaving the river each year, compared to what would be produced under "undisturbed" conditions), and that the cause of this shortfall is sufficiently well known that stocking appears to be an appropriate management option. A number of fundamental quantitative questions were identified, of which the most germane to this review is: "will the enhanced production of silver eel in the stocked population exceed the putative loss (from glass eels caught and used for stocking) in production from the donor population or, indeed, will production in the donor population increase because of reduced density-dependent mortality?"

ESAT can take eels from the glass eel stage, pigmented elvers or yellow eels of a larger size (native or stocked), and models their development through differentiation into male and female yellow eels (at sex-specific sizes) until they metamorphose into maturing silver eels and leave the catchment to return to the ocean to spawn. Throughout their freshwater residence, the yellow eels are subject to mortality that can vary with age and stage, allowing the user to account for elvers having higher mortality than older eels. The model calculates the size of the river's eel stock in terms of number of eels (population-wide or age-specific) as well as the biomass of escaping silver eels. Eels stocked after on-growing can also be included in the model, and estimates of the initial eel stock in the river system can be made.
This length-based model uses gender-specific probability functions (given in terms of length frequencies at a particular time after stocking, from which biomass can be calculated using corresponding length-weight relationships) to represent how plausible it is for an eel of a given length to undergo each of the key processes such as sex differentiation, silvering and escapement, which take place within specific length ranges (which depend on the sex of eels). It is assumed that density-dependent effects only take place when the density of eels is high enough to affect the role that key processes play in their population dynamics, and that there are no density-dependent effects in the areas in which stocking takes place (which should be chosen to maximise eel production from stocking). However, if such information is available, density-dependent rates/probabilities can be included in the quantitative formulas used to describe these processes.

Running forward, the model estimates the population of yellow eels or an annual biomass output of silver eels from a given level of stocking, spread over several years according to growth rates, sex ratios and ages at which male and female eels silver and leave the system. Running the model backwards (minimisation) will, therefore, provide an estimate of the annual input of stocked eels required to produce a given population of yellow eels or biomass of silver eels. In either case, steady state dynamics have to be assumed for the freshwater population (i.e. recruitment/stocking, growth, mortality and size/age at stage changes remain constant through the time period considered).

Whilst the model does not include the impacts of such issues as parasites, diseases, pollution, etc on eel production, it can accommodate putative changes in survival due to these factors by increasing the natural mortality values used in the model. Fishing mortality could also be treated similarly, though the EMPs' aim of maximising silver eel escapement would be best served by stocking only where eels are unlikely to be exploited.

In its end-user form, the model is initiated with parameter values that are appropriate to the UK (obtained from published and grey literature and which vary within and between catchments), and the user guide provides information on why the proposed values were chosen. The main inputs are the (additional) numbers or biomass of yellow or silver eels required to meet the management target, the density level and size/age at which eels are stocked, and density values that can be used as a reference to decide whether the density of stocked eels is approaching levels that can trigger density-dependent effects. Although this model has been made available to eel management authorities (the Environment Agency in England and Wales), there has been no attempt to compare silver eel production from translocating glass eel or stocking eels from an external source.
A similar, but more global (in time and space) approach is used in the TranslocEEL Stocking model, which uses data on the survival of eels from both source and stocked areas to assess the net benefit (or loss) of stocking in terms of spawner output, compared with the "do nothing" option, and is run over a number of generations (i.e. it includes estimates of spawning success). The model of Aström and Dekker (2007) and the SED model (Lambert, 2008) has been expanded to incorporate three geographical compartments with different levels of recruitment and production characteristics: West, North and South Europe. Put

simply, it is based on the combination of mortality lines (estimates of the life-span mortality for female eels from glass eel to silver eel in the historical situation - 1980–2005 – for each compartment) and a single stock–recruitment relationship (assuming panmixia). Additional information concerning glass eel mortality is needed for the donor compartment (which is always the West), whilst the mortality of stocked fish in the recipient compartments is adjusted relative to mortality of native fish. A full description of the model is presented in Annex 7 of ICES (2011b).

The biological features of female eels in each compartment (age at silvering, proportion of undifferentiated eel that become female, fecundity – potential egg production per female, capacity to reach the Sargasso Sea) and the proportion of glass eel arriving in each compartment are first defined. The stock–recruitment relationship is then fitted to mimic the observed trend in European glass eel recruitment (Aström and Dekker, 2007), though it should be stressed that this is not biologically validated against effective spawning biomass (as with most marine fish S-R relationships).

The main operational assumptions of the TranslocEel model are that there is no density-dependant regulation of mortality or sex ratio determination (as with ESAT, but clearly biologically unsound), and that the proportion of males is not a limiting factor for the population dynamics (i.e. female biomass and effective fecundity largely determines potential recruitment, so males are not included in the model).

The mortality coefficients for the West compartment are taken from estimates of all anthropogenic impacts in rivers on the French Atlantic coast (Lambert, 2008). The coefficients for the North are those published by Dekker (2000) based on catches from Europe “elsewhere than Bay of Biscay” and with a lifespan corresponding to northern latitudes. The lifespan mortality in the South compartment is the ratio of current escaping biomass to the best achievable escaping biomass for the French “Rhône Méditerranée” eel management unit (ICES 2010). The continental lifespan was fixed in accordance with the mortality estimates and the life parameter table developed by WGEEL (b, 2010a).

The fate of fish stocked into the three compartments is adjusted to take account of post-fishing mortality of 20% (Briand *et al.,* 2009) and an additional 5% mortality during transport and quarantine. ICES (2011) could find no clear evidence of a difference in mortality between native and stocked fish in the same environment.

The oceanic journey for leptocephalus larvae was fixed at two years, and the proportion of glass eel recruitment arriving in each compartment was assumed to be constant over time and based on Bonhommeau *et al.*’s (2010) interpretation of leptocephali distribution.

Data from three index countries were used to determine the length and age of silver eel escaping from the three compartments (ICES 2010): France for the West (average length of females at silvering = 67 cm); Sweden for the North (average length of females at silvering = 73 cm); and Italy for the South (average length of females at silvering = 60 cm). The proportion of undifferentiated eel that become female was estimated as 81%, 98% and 73% for the West, North and South compartments, based on the sex ratio of silver eels escaping from France (4:6 M:F), Sweden (1:9) and Italy (1:1) respectively for the period 1980–2000, back-calculated to undifferentiated eel using the continental lifespan of males and females and the lifetime mortality of each sex.

It has been estimated that about 20% of silver eels leaving the Baltic Sea will arrive with a net content of fat of 0% (Clevestam *et al.,* 2011). Applying these values for the North compartment to the corresponding length and distance data for the West and the South compartments, indicated that 18% of silver eel from the West, and 28% from the South compartments are also probably unable to spawn successfully by the time they reach the Sargasso Sea. Specific fecundity (to drive the life table, but effective fecundity is not known) and capacity to reach the Sargasso were standardized relative to the values calculated for the West compartment, so silver eel numbers are expressed in terms of 'West females'.

During model calibration, the net reproductive output was estimated to be one West silver eel escaping from 30.5 glass eels, lower than the values of 121 glass eels per silver eel found by Bonhommeau *et al* (2009) and 149 glass eel per silver eel of Andrello *et al.* (2011), both based on a steady state hypothesis.

A number of scenarios were tested by WGEEL (ICES, 2011b) which illustrate the utility of this approach, though the assumptions and biological unknowns attending this model should be borne in mind. In a scenario representing the historical conditions, where anthropogenic mortality is high in all compartments, stocking of glass eel appeared to have no long-term benefit in any compartment, but neither does the option of not translocating eels in the first place lead to a sustainable return, whether or not the corresponding fishing mortality is reduced.

A scenario representing a situation where conservation measures have been implemented across Europe and anthropogenic mortality in all compartments is sufficiently low that the global eel population will not crash (i.e. it is stable in the long term, and recruitment is not declining), revealed that by far the best measure both in the short (15 years) and long run (50 years) is where there is no stocking and fishing mortality of glass eel is reduced, corresponding to the level that would have been used to supply stocking. In this scenario, glass eel recruitment will increase in the West compartment. When the fishing mortality corresponding to stocking is not reduced, the glass eel recruitment stabilizes over 50 years at a relatively high level, but does not increase. Stocking with glass eel into an area in the West other than the donor catchment produces a stable return at a slightly increased level, whilst stocking in the North or South European compartments also produces a stable return, but at lower levels.

The results of this exercise suggest that the only situation in which increased numbers of glass eel are produced in the long term (through a number of life cycles) is when the glass eel are left *in situ*, and the corresponding mortality in glass eel and elver fisheries is effectively reduced. All other situations lead, at best, to a stabilization of the population (at the current depressed level, i.e. no recovery). When comparing stocking locations, the outcome is always better when the glass eel are stocked in the source (West) compartment rather than North or South compartments.

This model appears to be largely driven by the fate of recruiting glass eels, since it is not sensitive to population dynamics at the yellow eel stage (which are fixed for each compartment) or any influence other than apparent female stock size on recruitment *per se*. Unsurprisingly, WGEEL (ICES, 2011b) concluded that this model is very sensitive to parameter calibration, and that the outcomes of this modelling exercise are not definitive. They do, however, illustrate the macro-effects of the various management options, in particular changes in the fishing effort on glass eels and stocking versus leaving eels to recruit naturally.

Discussion and conclusions

ICES has provided advice on stock status of temperate marine species and salmon and management of their fisheries for up to 50 years, but has a relatively brief history of providing conservation advice for eels (10 years), and there is considerable uncertainty surrounding some of the assumptions behind the advice. In particular, ICES has concerns that stocking glass eels is unlikely to contribute to the recovery of the European eel stock because (a) there may be no surplus of glass eel to be redistributed to other areas and (b) there is evidence that stocked/translocated eels experience impairment of their navigational abilities (ICES 2011a). It could be concluded that ICES advises that stocking should not be carried out and, as a result, there is now pressure to do less rather than more re-stocking.

In its latest report, WGEEL (ICES, 2011b) considered that current information on growth, sex differentiation, maturation, silvering and migration to the continental shelf has not shown any major differences between stocked and native eels. In particular, that as far offshore as eels have been tracked, coastal and oceanic migration routes and behaviour patterns of eel of stocked origin are indistinguishable from those derived from naturally immigrated recruits. The Working Group's conclusion appears to be that stocking has the potential to produce emigrating silver eel, which this review has endorsed. The most recent advice from ICES (2011a) is that new information available (from WGEEL) on the risks of translocating eels does not change the advice on the potential of stocking. This is that, though current glass eel stocking programmes are unlikely to contribute substantially to the recovery of the European eel stock (compared with closing all fisheries, or opening obstacles to migration, for example), all catches of glass eel should be used for stocking, which should take place only where survival to the silver eel stage is expected to be high and escapement conditions are good.

WGEEL's review of eel stocking in 2011 (ICES, 2011b) led it to consider that stocking is only acceptable as a means to assist overall recovery of a panmictic stock (such as European and American eels), rather than to maintain fisheries. As stocking is permitted and occurring under the terms of the EU eel regulation (EC, 2007), there is an argument that one should also seek to produce sustainable fisheries, but these must be supported by a stock that is itself sustainable. From a scientific point of view, therefore, the ultimate goal of any stocking exercise is one of ensuring net benefit for the whole stock.

Though the results of ICES' (2011b) TranslocEel model runs must be viewed with caution, they do indicate that stocking may not make the most efficient use of the glass eel cohort compared with the option of leaving them *in situ* to recruit naturally, where this is combined with a reduction in fishing mortality corresponding to that which would have accounted for the glass eels used for stocking. Given the current assessment of the overall stock, and the option of stocking within the EU Regulation, where it occurs, stocking should be done in conjunction with measures maintaining or improving spawner escapement, through reductions in fisheries (yellow and silver) mortality and other direct mortalities (e.g. turbine, pumping stations) affecting the stocked eels. This could be interpreted as reflecting the first scenario explored above with the TranslocEEL stocking model, which indicates that anthropogenic mortality has to be reduced in order to enable any recovery of the European eel.

It must be stressed here that, where WGEEL has based its comments and advice on the outcome of a modelling exercise, due notice should be taken of the model's sensitivity to parameter choice and assumptions, though eel population models are becoming quite sophisticated in relation to their reflection of the species' life history (continuing doubts about silver eel migration and spawning dynamics notwithstanding). The models can, however, be used to indicate where we should look for evidence of the success or otherwise of stocking, and help to explain or validate empirical data and information, which is the object of this report.

The EU eel Regulation contains an obligation that some 60% of the national catch of eel less than 12 cm is used for stocking (by 2013), and WGEEL (ICES, 2011b) recommends that these glass eels should be stocked in areas where anthropogenic mortality is minimal and environmental quality is high. Importantly, WGEEL observed that the burden of proof that stocking will generate net benefit in terms of spawner escapement rests with those taking the stocking action (this review should help here), and suggests that a risk assessment should be conducted prior to stocking, taking into account fishing, holding, transport and post-stocking mortalities and other factors such as disease and parasite transfers. It is difficult to understand what should happen if this proof is lacking (no stocking?). Interestingly, WGEEL concluded that the performance of stocked grown-on eel cannot be assumed to be as good as that of natural immigrants (once they have reached the yellow eel phase, presumably), though it does often fall within the ranges of best and worst observations of performance of native stock. This review supports this contention, and suggests that the additional expense of rearing, on top of the high prices attracted for glass eels, is not cost-effective.

Symonds' (2006) review of the need for and feasibility of enhancing American eel populations by stocking includes a step-wise approach to planning a stocking programme (after Cowx, 1999), which starts with the preposition that a decision not to stock is not necessarily the wrong decision and asks whether enough information is available to justify initiating stocking. For the European eel, we can accept that stocking is taking place, and encouraged by the ERP, but it is useful to note some of the questions posed in Symonds' aide memoire that are relevant to the last question (and the present review). The European Commission has defined the aims of a stocking programme (EC Regulation EU COM 1100/2007), based on stock assessments of European eel that clearly indicate where the population is in need of enhancement (EMPs). A wealth of information is available to demonstrate that stocking can produce eels that survive to silvering, and the questions of glass eel and elver supply and financial and human resources and expertise available to carry out stocking have been or are being addressed. Of Symonds' remaining questions, the most pertinent are similar to those raised in the introduction to the current review, the answers to which are summarised below (the number of papers considered in this review that provide specific information on each issue is indicated, which gives some idea of the level of scientific evidence available):

- *is **survival** of stocked eel to escaping silver eel lowered (to the extent that there may be an overall loss to spawner production)?* This is extremely difficult to answer, mainly because experiments in translocating eels, accompanied by controls without translocation, have not been carried out, though models exist that might provide indicative outcomes. Given the considerable evidence that stocked eels do survive and escape as silver eels, it is logical to assume that enhancing eel populations throughout the species natural range where recruitment has been poor, must increase overall production. In assessing any net benefit of stocking glass eel, however, we need to include losses from fishing, transport and storage (before they are stocked) - not just look at the survival of glass eel once stocked (29 papers).

- *are there differences in the **growth rate** of stocked and native eel that may lead to an overall loss of biomass of escaping silver eel (to the extent that there may be reduced spawner production)?* Probably not. Even if stocked eels do grow more slowly than native eels (for which there is no evidence), density effects on growth and sex ratio are more likely to influence growth rates and eventual biomass production (19 papers).

- *is there evidence that stocking with eel actually leads to an overall increase in **yield** (of yellow or silver eel)?* The results of studies that estimated yield per recruit (and yield per unit area) for stocked glass eels indicate that yields within the range 20-70 g per recruit (4-14 kg per hectare, at a nominal stocking density of 200 glass eels per hectare) might be expected. Higher yields quoted for some studies may be associated more with potential fishery yield than eventual silver eel escapement, and there is obviously a confounding effect on yield of stocking density and potential productivity of the water body into which eels are stocked. Therefore, stocking with eels does lead to a quantifiable increase in yield of yellow or silver eel in the stocking location, but we cannot say whether this is an overall increase compared to leaving the glass eels in situ (and not catching them for purposes other than stocking) (26 papers).
- *does **on growing** in aquaculture facilities before stocking out confer any benefit?* Generally not, but holding glass eels with at least maintenance feeding until the time that

they can be stocked with a good chance of survival in otherwise cold or ice-bound northern waters is a positive option (20 papers).

• *how does stocking density influence the above?* The available evidence shows no clear relationship between stocking density and yield, which probably reflects the variations in stocked waters' carrying capacity for eels and also in the various studies' protocols (22 papers).

• *might changes in the **sex ratio** of eels as stock density changes represent a risk to reproduction (during spawning)?* We simply do not know, chiefly because the influence of sex ratio at spawning is not known, though it might be presumed that a shift towards females would result in higher overall population fecundity. The default strategy would be to stock in such a way that local densities mirror those that obtained during the period when recruitment was high (1950-1970), if known (10 papers).

• *do stocked eels actually contribute to spawning escapement?* There is good (if indirect) evidence that stocking has resulted in a proportional increase in escaping silver eels, though estimates of effectiveness vary depending on the growth area (fresh, brackish or marine waters) and barriers to emigration (11 papers).

• *are there differences in somatic (size, fat content) and reproductive factors (maturation indices, fecundity) that might result in lower spawning success in stocked eels?* There is little evidence of any consistent difference between (presumed) stocked and native eels (but only 5 papers).

• *are there behavioural impairments (e.g. migration, spawning) due to translocation that could reduce the success of spawning?* Again, we simply do not know, though there is evidence that the migratory behaviour of stocked-origin silver eels is similar to that of native eels. It would be prudent, however, to ensure that stocking results in well dispersed eels and only occurs where there are few if any obstacles to sea-ward migration (19 papers).

• *is there a risk of spreading of **disease** and **parasites** when eels are moved from one area to another?* Yes, as with any translocation of living material. This can be minimised, however, by using glass eels caught by fishing methods that cause the least damage and transporting quickly in conditions that avoid undue stress (density, water quality, temperature). If it is considered necessary to hold eels prior to stocking, it is advisable to start with good quality glass eels (free of parasites and disease, and from areas with low chemical contamination risk) and to use quarantine facilities where eels can be screened and tested, if necessary (18 papers).

• *could the **genetic** structure of eel populations in recipient waters be altered by introductions of eels from elsewhere?* This seems unlikely, given that the European eel population is thought to be essentially genetically unstructured (panmictic). Any genetic variation due to temporal and spatial sub-structuring within recruitment (which is inevitable) is likely to be minimised by stocking either locally (within RBDs or countries, for example) or where eels no longer recruit naturally (but growth and escapement opportunities are good) (13 papers).

The results of any review are always open to re-evaluation as new studies are completed, written up and published and, in this respect, the above conclusions can be regarded as setting a benchmark derived from the scientific (peer-reviewed) evidence available up to May 2012. This enables us to challenge what we do and do not know about the benefits of stocking, to make decisions about the most rewarding focus of new work, and to judge new results as they become available. It is clear, for example, that new genetic work on *A. anguilla* is unlikely to provide information that has an immediate practical use in stock recovery, and that the EELiad project (and its successors, especially work on maturation and "fitness" for migration and spawning) should place as much emphasis on stocked-origin eels and on native eels, in the Mediterranean as well as northern Europe, since this has obvious relevance to our understanding of the potential contribution of stocked eels to the population's reproductive capacity (i.e. do they produce recruits?).

ICES has adopted the precautionary approach in assessing the potential influence of the various factors affecting the eventual production of spawning eels from stocking and the risk that this might entail. The precautionary approach, however, may be applied differently by fisheries policy-makers and managers in different countries, reflecting the diversity of problems faced. One, general, view is that action (to protect stocks from detrimental impacts) should not be delayed where there is uncertainty that the action will succeed, and this is probably the thinking behind the stocking option in the Commission's ERP. With respect to transfer and stocking of eel, however, it could also be interpreted as: do not take action (stocking) where there are uncertainties over whether or not this will result in viable spawners. A third argument could be: stocking is expensive, and potentially risky in terms of net benefit.

It is clear that, despite a considerable body of information, we still do not have unambiguous answers to most of the issues mentioned above, chiefly because very few studies have been carried out in a controlled way. To help future decisions (and following WGEEL's recommendation), documented assessments of the risks of stocking should be carried out (with explicit scientific input), both to judge whether stocking should take place and to assist with post-stocking monitoring. The latter should aim to assess whether stocking has been successful in achieving its objectives (usually sadly lacking) and, if adverse effects of stocking are encountered, to guide corrective measures.

In principle, the size (life-stage) of eel used for stocking should preferably be that which maximizes the yield of escaping silver eels in relation to stocking costs, which depends to a large amount on the fishery, availability and costs of native eels (from glass eels to small yellow eels). This review suggests that there are advantages of stocking with glass eels/ elvers because of the larger numbers available (though in a limited season), that have not been subject to local density-dependent and habitat influenced mortality, lower risk of disease and parasite transfer, lower transportation costs, and lower impact on local donor populations at recipient sites. The advantages of stocking with small yellow eels (wild-caught) are a lower mortality after stocking, a more predictable outcome, shorter time before spawning escapement and, possibly, later relocation could facilitate seaward migration.

Symonds (2006) suggests that, as little is known about the effect of timing of arrival and migration patterns of glass eel on growth rates and sex determination of the adult eel, collections for stocking of only a discrete portion of any one glass eel/elver year class should be avoided. This equally applies to any variation in genetic structuring, and can be smoothed if collections are made over the length of the inward migration season and over a number of years.

With respect to ICES' concern that stocked/translocated eels experience impairment of their navigational abilities, this review has provided evidence that stocked eel will, in productive environments, produce yellow and silver eels which will attempt to migrate, as did the review of Wickstrom *et al*. (2010). These authors found that, while there are some examples where emigration of previously stocked eels is less successful than from native recruits, there are many more cases where translocated eel appear to have emigration behaviour that mirrors that of the natural eel to the furthest point at which naturally recruited eel have been observed. Eels bearing data storage tags originating in wholly stocked populations were tracked out from the Baltic and showed the same oceanic migration behaviour and the diel vertical migration found by native eels carrying satellite and data storage tags.

As yet, however, no eel, let alone one of stocked origin, has been followed to the spawning grounds. Even if work within the EELIAD project succeeds in this, and because only modelling studies are currently able to quantify (albeit with considerable scope for uncertainty) the contribution of stocked eels to the next generation of glass eels compared to leaving glass eels to recruit naturally, I suggest that we do not yet know whether there is any net benefit of translocation and restocking to the European eel population. This does not, however, mean that there are no benefits to be gained from stocking. As long as glass eels in some estuaries that continue to receive substantial recruitment are prevented from ascending local rivers because of permanent barrages, catching and translocating them with minimal mortality to productive habitats, from which they can escape back to the sea, must be a beneficial option. A less quantifiable option, stocking European eels in those parts of their natural post-glacial distribution range where there is currently no or little recruitment and where phenotypic variation can be maximised (warm saline lagoons in the eastern Mediterranean; oligotrophic freshwater lakes in Scandinavia, for example), is also likely to benefit the species by ensuring diversity in the spawning population.

This review has highlighted two areas where future research could be considered a priority. One is the need for controls when investigating the yield of silver eels from stocking compared to leaving glass eels to recruit naturally. It is not easy to envisage how this could be done experimentally, but there are several population models that could now be used to provide quantitative answers, given robust parameterisation. The second area is further examination of the fitness (for reproduction) of silver eels originating from stocking compared to native eels, and of their migratory behaviour and capability to reach the spawning grounds, comparing eels in northern and southern continental Europe, north Africa, the eastern Mediterranean and along the Atlantic coast.

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