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Reflections on the decline and management of European eel*

Überlegungen zum Rückgang und Management des Europäischen Aales

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Summary: In response to the dramatic decline of European eel, the European Commission implemented an eel recovery plan (EC 1100/2007) which obliges each member state to identify eel catchments and to apply management measures to return the eel stock to sustainable levels. This management comprises substantial uncertainties, because several aspects of eel's life history still remain unknown, primary causes of decline are not fully clarified, and only a few of the potential causes for decline can be addressed by management measures in freshwaters. This study briefly reviewed the most recent literature and discussions on the causality of eel decline with regard to rehabilitation measures. Research needs have been identified in determining the relative contribution of freshwater grown eels to the spawner stock. Current studies provided some evidence that not all migrating silver eel perform a catadromous life cycle and that eel spawner may primarily recruit from marine or coastal habitats. If the latter becomes scientifically confirmed it seriously calls the potential into question managing eel recovery in the designated freshwater catchments and would rather support increasing the glass eel escapement instead of stocking.

Keywords: European eel *Anguilla anguilla*, eel decline, European Eel Regulation, eel stock management, glass eel

Zusammenfassung: Die Europäische Aalverordnung (EC 1100/2007) verpflichtet alle Mitgliedsstaaten zur Ausweisung von Aaleinzugsgebieten und zum Ergreifen von Maßnahmen zur Hebung des Aalbestandes. Dieses Aalbestands-Management ist mit erheblichen Unsicherheiten behaftet. Neben den bislang noch immer unbekannten Aspekten insbesondere in der marinen Phase im Lebenszyklus des Aales, sind auch die primären Ursachen für den Aalrückgang noch ungeklärt und können nur einige der potentiellen Ursachen im Süßwasser gemanagt bzw. beeinflusst werden. Im Rahmen dieser Übersicht wurde die aktuelle Fachliteratur und Diskussion zu den Ursachen des Aalrückgangs in Bezug auf mögliche Förderungsmassnahmen ausgewertet. Dabei hat sich die Aufklärung des Beitrags der im Süßwasser aufgewachsenen Aale zum Laicherbestand als wesentlicher Forschungsbedarf herauskristallisiert. Es gibt zunehmend Hinweise, dass sich die Laicherpopulation des Aals vorwiegend aus dem marinen und Küstenbereich rekrutiert, was die Möglichkeiten einer erfolgreichen Förderung des Aals in den ausgewiesenen Binneneinzugsgebieten zumindest in Frage stellen würde. Wenn diese Hypothese wissenschaftlich bestätigt wird, sind die steigenden Besatzzahlen in den Aaleinzugsgebieten zu überprüfen, zugunsten größerer Anteile der ankommenden Glasaale die im Gewässer verbleiben und sich natürlich ausbreiten können.

Schlüsselwörter: Europäischer Aal *Anguilla anguilla*, Aalrückgang, Europäische Aalverordnung, Aalbestands-Management, Glasaal

*Dedicated to our coauthor Prof. Dr. F. Kirschbaum on the occasion of his 65th birthday and retirement

1. Introduction

The global European eel *Anguilla anguilla* stock has dramatically declined in most of its distribution area and is considered outside safe biological limits (FAO & ICES 2009). Today (mean 2004-2008), the average eel recruitment ranges between 1% (North Sea) and 10% (British Isles) of the 1970s reference level, and the yellow eel stock e.g. of the Baltic Sea is at 6% of the 1970s level and at 8% of the 1950s level, with none of the 28 time series studied showing any sign of recovery (FAO & ICES 2009).

Because of this large scale decline in glass eel since about 1980 and in young yellow eel since the 1950s, an eel recovery plan has been initiated by the European Commission (Council Regulation EC 1100/2007) to return the eel stock to sustainable levels of abundance and recruitment. Each member state was obliged to identify and designate eel catchments, to develop Eel Management Plans until December 2008, and to start with suitable rehabilitation or management measures in 2009. European eel management aims to achieve an escapement of silver eel spawners corresponding to at least 40% of the biomass expected to be produced under environmental conditions with no anthropogenic disturbance.

Achieving this objective faces major challenges. Firstly, several aspects of the eel's complex life history still remain unknown or poorly understood, e.g. spawning eel or eggs have never been observed in the wild (Tesch 2003, Dekker 2008). European eels are considered catadromous species growing and reaching maturity in freshwaters and spawning in the Sargasso Sea (Tesch 2003). Secondly, the primary causes of the eel decline are not fully clarified (Russel & Potter 2003, Dekker 2004, 2008) ranging from environmental changes in the spawning area (Bonhommeau et al. 2008) and shifted oceanic conditions (Knights 2003, Friedland et al. 2007) to pollution, habitat fragmentation or overexploitation in the freshwater habitats (Feunteun 2002). Accordingly, thirdly, only a small proportion of the potential causes for decline could be efficiently managed in the freshwater eel catchments. Fourthly, due to the longevity of eel and its long generation time, there might be substantial lags between impact and decline as well as measure and recovery (e. g., Åström & Dekker 2007). Finally, without quantifying potential impacts at all stages of the eel's life cycle and without identifying and addressing the essential bottlenecks for eel recruitment or mature silver eels, there is a high risk of failing to rehabilitate the European eel stock.

Eel is of high socio-economic and cultural value and one of the most important species in commercial and recreational inland fisheries throughout Europe (Ringuet et al. 2002, FAO & ICES 2009, Dorow et al. 2010). Thus, a precautionary approach in eel rehabilitation should not only account for uncertainties in the relative contribution of various simultaneously acting factors to the eel decline (Russel & Potter 2003, Åström & Dekker 2007, Dekker 2008), but also for socio-economic objectives and potential economic and cultural losses (sensu Acheson 1981). However, both, the socio-economic importance of eel and eel fisheries as well as the challenges of a European-wide management of the panmictic eel stock (Dannewitz et al. 2005, van den Thillart et al. 2005) considering various, often opposing member state interests were not in the narrower focus of this study. Going one step back, the primary reasons for decline have to be identified first before negotiating rehabilitation efforts and their potential socio-economic impacts.

This review aimed to briefly summarize the actual scientific discussion of causes for decline, management options, and potential recovery to identify remaining knowledge gaps, and to draw considerations about successful eel management mainly from an ecological perspective.

2. Potential impacts and bottlenecks

The complex life history of eel provides several stages during their oceanic and continental life phase, where pressures could solely or in combination impact on eel recruitment, abundance and spawner stock development, which have been conceptualized in figure 1. Several reasons for decline have been discussed already, like habitat loss, degradation and fragmentation (FEUNTEUN 2002, BRUIJS & DURIF 2009), climate change related shifts in the oceanic conditions (KNIGHTS 2003, FRIEDLAND et al. 2007), pollution (ACOU et al. 2008), contaminants (VAN GINNEKEN et al. 2009, GEERAERTS & BELPAIRE 2010), the swimbladder parasite *Anguillicola crassus* (KIRK 2003), viruses (VAN GINNEKEN et al. 2004, 2005b, VAN DEN THILLART et al. 2005), overexploitation (DEKKER 2003a, CICOTTI 2005), predation by fish-eating birds (KNÖSCHE et al. 2004, ZYDELIS & KONTAUTAS 2008), or spawning stock depletion (DEKKER 2003a, FAO & ICES 2009), especially of male eels (KETTLE et al. 2008, BELPAIRE et al. 2009).

All the factors identified simultaneously influence the eel stock, however, their relative contribution to the eel decline remains unknown and they may further vary in strength depending on the geographic region.

2.1. The oceanic phase

The marine part of eel's life history largely remains a mystery. Because neither spawning nor eggs have been ever observed in the wild (TESCH 2003, DEKKER 2008), information are lacking on basic reproductive parameters like egg quality, egg mortality, fertilization rate, hatching rate, and larvae survival. BONHOMMEAU et al. (2008) reported a positive correlation between the glass eel recruitment at the European coast and the primary productivity in the Sargasso Sea, while variations in latitude and strength of the Gulf Stream did not explain variations in glass eel recruitment. BONHOMMEAU et al. (2008) have identified a regime shift in sea temperature that preceded the start of the decline in glass eel recruitment which was

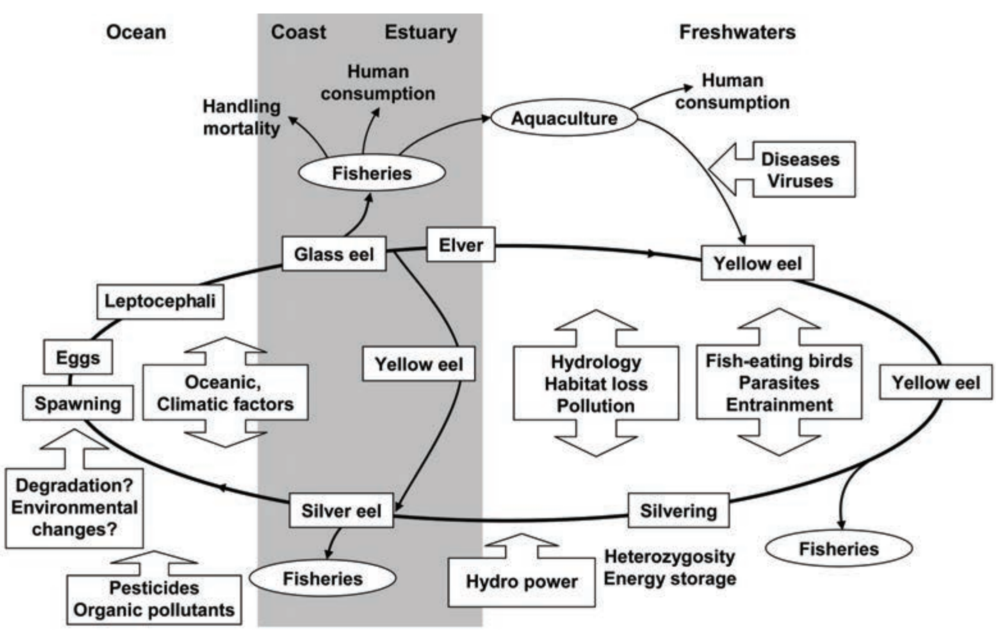

Fig. 1: Conceptual framework of the spatial distribution of the different life history stages of eel and potential influences and causes of decline.
Abb. 1: Konzeptionelle Übersicht zur räumlichen Verteilung der verschiedenen Lebensstadien des Aales und der potenziellen Beeinflussungen und Rückgangsursachen.

inversely correlated to primary productivity and have concluded a strong bottom-up control of leptocephali survival and growth by primary productivity in the Sargasso Sea. Correspondingly, changed oceanic conditions were considered to influence the food web and nutrient conditions for the eel larvae, their survival and transport towards the Gulf Stream (KNIGHTS 2003, FRIEDLAND et al. 2007), but also the selection of spawning sites or areas by silver eel (FRIEDLAND et al. 2007). However, the Sargasso Sea provides a highly dynamic environment with a permanently stratified tropical part and a northern or subtropical part where frequent mesoscale eddies and winter convection sustain new primary production (LIPSCHULTZ et al. 2002). There is some evidence for the existence of more than one spawning site most probably south of the subtropical convergence zone (reviewed in VAN GINNEKEN & MAES 2005), but as far as the spawning site selection in eel remains unknown, environmental constraints, food deprivation or increased predation in the spawning and nursing areas cannot be excluded as primary reason for the eel decline.

Leptocephali of the European eel drift from the Sargasso Sea with the Gulf Stream and approach the coastal shelf of Europe and North Africa mainly in the Biscay area. This area comprises less than 10% of the total distribution area of eel and produces only 10% of the silver eel biomass but receives three-quarters of all recruitment (DEKKER 2000). Weakening and shift of the north wall of the Gulf Stream linked to global climatic changes were suggested to reduce the migration success of leptocephali since these larvae have to follow longer more northerly routes (KNIGHTS 2003). Although not detected by BONHOMMEAU et al. (2008) in their analysis, this might become more evident in time series analyses using data from northern or edge populations. Very little is known about the leptocephalus phase and its passive transport and the little that is known is largely beyond the influence of management. Current approaches to estimate the recruitment success and the number of recruits per migrating silver eel (e.g., ÅSTRÖM & DEKKER 2007) remain uncertain and hardly verifiable guesses, as far as they base on limited information about natural mortality in leptocephali, significant deficiencies in assessment of both glass eel recruitment and silver eel stock (FAO & ICES 2009), and also partially unreliable total landing data (ICES 2009).

2.2. The continental phase

Having arrived on the continental shelf, leptocephali metamorphose into glass eels, an unpigmented stage, which disperse along the coasts and colonize coastal, estuaries and to a certain proportion inland waters. Their subsequent growth period, the feeding or yellow eel stage is the longest phase in their life cycle and lasts 3-8 years in males and 8-15 years in females until silvering depending on the environmental conditions (TESCH 2003, ÅSTRÖM & DEKKER 2007, DEKKER 2008). The continental phase is the best studied so far, during which eels face potential impacts from numerous stressors.

2.2.1. Glass eel fishery

Glass eels are exposed to an intense fishery harvesting between 800-900 t (FEUNTEUN 2002), 350-525 t (FROST et al. 2001), and actually about 100 t a year (FAO & ICES 2009), which are used for restocking, aquaculture and direct consumption. The sharp decrease in volumes will further increase the fishing pressure because it has been more than counterbalanced by the increase in glass eel price from 100 Euro kg^{-1} in 1989 to 750 Euro kg^{-1} paid to the fisherman at the beginning of 2008 (BRIAND et al. 2008).

A substantial proportion of the glass eel catches goes directly to human consumption. In the 1970s approximately 1000 t of glass eels were processed for human consumption (EFSA 2008), in the 1990s about 125 t of 580 t total landings (DEKKER 2003b). In 2006 it was estimated that of a total catch of 120 t glass eels for the whole of Europe approximately 25-30 t were utilized for aquaculture, 60 t shipped to Asia, 1 t used for re-stocking in Northern Europe, and the balance of about 29-34 t killed in the process of capture and retained for human consumption (EFSA 2008). Glass eel fisheries suffer from significant handling mortalities, monitored by Briand et al. (2009, cited in ICES 2009) in the Vilaine Estuary in 2007. This study reported average glass eel mortalities of 42% (2-82%) within 48 hours following the push net fishery. In contrast, zero mortality was found in glass eel obtained from fish ladders or collected by the traditional hand nets (Briand et al. 2009, cited in ICES 2009). Thus, the large scale replacement of traditional fisheries by a highly efficient push net fishery in the 1960s might have contributed to overharvest and decline of eel recruitment as well. However, no data were available whether or not these losses become simply discarded, or appear somewhere in the catch statistics, directly among those glass eels used for consumption, or indirectly by increasing the stocking content in aquaculture production or by contributing to hidden failures of stocking in the wild.

Aquaculture of European eel is fully based on glass eel catches. It started in the all-time high of glass eel yields in the early 1970s (Ringuet et al. 2002) and has rapidly developed. The annual demand of glass eel for European eel farms was 35-45 t between 1995 and 1999 (Frost et al. 2001) allowing for an eel production of 9000-11 000 t in aquaculture. In Europe eel culture reached the peak of production (FAO & ICES 2009) with reported 10 510 t in 2000 (ICES 2004), while the actual aquaculture production of eel ranged between 8000 t and 9000 t in 2006 (FAO & ICES 2009).

In 2000, additional 10 000 t of the European eel have been produced in Japan (ICES 2004). If one kilogram of glass eel is raised to on average 200-250 kg (maximum 385 kg) in eel farms (Frost et al. 2001), the peak production has demanded between 27 t glass eel at maximum productivity and 53 t on average. Additionally, about 40-50 t were required for the eel production in Japan assuming comparable aquaculture technologies. However, the export of glass eel to Asia was reported to have stabilized at 110-120 t between 1997/98 and 1998/99, while the real amount was estimated at 250 t in the 1997/98 season and at 140 t in 1998/99 (Frost et al. 2001). Briand et al. (2008) reported on average 123 t per year exported to Asia during the period 1996-2006. Additional 38 t glass eels were transported to Northern Europe, of them about 3 t directly used for stocking. In 2006, in total 94% of the glass eel trade has been finally used in aquaculture (Briand et al. 2008).

Beside this there were substantial non-commercial and other unreported landings. For example, Portugal surprisingly appeared as glass eel producer, despite this fishery is illegal there (Briand et al. 2008). According to Briand et al. (2008), Portuguese fishermen have exported significant amounts of live glass eels in 2006: 36 t to Asia, 32 t to Northern Europe, 3 t to Spain for consumption, and 1 t for restocking.

Incomplete time series, unreliable data sets, landing data which widely vary between the available statistics and sources, and a substantial amount of unreported catches, all hampers the assessment of the actual eel recruitment.

2.2.2. Yellow and silver eel fishery

After growing for several years yellow eel become exploited by fisheries. In Europe, the total commercial eel landings reported by the countries – yellow and silver eel together – were about 2600 t in 2007 (FAO & ICES 2009). A substantial but widely unrecorded amount is additionally harvested by recreational and other non-commercial fisheries. For example, estimations of anglers' yields in Belgium, The Netherlands and Germany revealed an additional harvest of in sum about 660 t per annum (ICES 2009). In some regions the recreational eel harvest may exceed the commercial (Dorow & Arlinghaus 2009). Non-commercial glass eel and yellow eel catches have been estimated at about one third of the commercial catches (FAO & ICES 2009).

2.2.3. Habitat loss

Especially in their freshwater habitats, yellow eels face additional threats from habitat loss, habitat fragmentation and habitat degradation, and migration barriers. In Europe, all larger river systems are heavily fragmented by thousands of dams and weirs (NILSSON et al. 2005) and more than 90% of their floodplains are functionally extinct today (TOCKNER & STANFORD 2002) resulting in significant losses in fisheries productivity.

About one third (42 000 km²) of potential eel habitats has been considered as inaccessible today (DEKKER 2008, FAO & ICES 2009). Limited habitat and food resources might prevent eel from reaching a sufficient fat content to successfully migrate to the Sargasso Sea and to reproduce (BELPAIRE et al. 2009).

After a regionally different number of years in freshwaters, up to 10 or 18 in males and females, respectively, eels metamorphose again (silvering) and transform to their migratory life stage. In particular during their downstream migration – predominantly from September to November – silver eels face significant mortalities, although the downstream migration occurs in a rather narrow timeframe, with less than 20 days having >50-75% of the total eel run (BRUIJS & DURIF 2009). Beside silver eel fishery, all kinds of barriers provide major obstacles for downstream migrating eels and in particular the passage of dams >10 m height, pumping stations and hydropower turbines cause significant mortality. Becoming entrained by a modern pump is 100% lethal, and up to 50%, commonly 22-38% of hydropower turbine-passing eels may be killed depending on the type of turbine (reviewed in BRUIJS & DURIF 2009). EBEL (2008) has reviewed 34 hydropower stations throughout Europe and reported average damage rates in eel of 44.6% (Kaplan turbines) and 42.9% (Francis turbines). Accordingly, a series of hydropower schemes along a river may cause dramatic losses of spawner biomass in total.

2.2.4. Pollutants

In European river systems, lipophilic pollutants and contaminants are widely accumulating in fish, especially in eels with their naturally high fat contents, where they significantly impact on spawner quality and migration performance, even at levels far below the maximum allowable for fish consumption (SVEDÄNG & WICKSTRÖM 1997, ROBINET & FEUNTEUN 2002, PALSTRA et al. 2006, GEERAERTS & BELPAIRE. 2010). During migration, lipid remobilization returns accumulated persistent lipophilic contaminants back into circulation system where they damage vital organs and germinal tissue (LARSSON et al. 1990), and concentrate in the gonads where they can cause various deficiencies in ovaries, vitellogenesis, or embryonic development resulting in decreased spawning success or egg survival (ROBINET & FEUNTEUN 2002, PALSTRA et al. 2006, VAN GINNEKEN et al. 2009, GEERAERTS & BELPAIRE. 2010). For example, by examining the toxic potency of dioxin-like organic pollutants using an in vitro reporter gene assay, PALSTRA et al. (2006) have determined significantly lower survival periods of fertilized eggs already at accumulations far below the maximum allowable level for fish consumption of 4 ng kg^{-1} fish.

2.2.5. Parasites and viruses

Infections by parasites and viruses were found to significantly lower the swimming performance of silver eels (VAN GINNEKEN et al. 2005b, PALSTRA et al. 2007). All eels from freshwater and brackish habitats have a high prevalence of *Anguillicola crassus* infections (JAKOB et al. 2009). Simulated migration trials in swim tanks revealed that 43% of eels with swim-bladders damaged by parasites stopped swimming at low aerobic speeds (<0.7 m s^{-1}) and showed early migration failures at less than 1000 km distance simulated (PALSTRA et al. 2007). However, in contrast to initial assumptions (KIRK 2003) parasitism at whatever level does not modify the pressure resistance of yellow eels (VETTIER et al. 2003).

Correspondingly, during an experimental simulation of silver eel migration in a large swim tunnel, eels infected with the rhabdovirus EVEX (Eel Virus European X) died after 1000-1500 km, whilst virus-negative individuals swam 5500 km, the estimated distance to the spawning ground in the Sargasso Sea (van Ginneken et al. 2005b). So far, three viruses, EVEX, HVA (*Herpesvirus anguillae*), and EVE (Eel Virus European) have been detected in wild and farmed European eels (van Ginneken et al. 2004).

Raising eels to fingerlings in fish farms before stocking yields high risk of virus infections.

2.2.6. Cormorant predation

The European, since the 1990s continuously growing cormorants *Phalacrocorax carbo* population has been discussed as major source of eel decline too (e.g., Cowx 2003, Knösche et al. 2004, FAO & ICES 2008). Eel consumption by cormorants has been estimated to 4000-6000 t a year corresponding to 30-50% of the 1993/1994 commercial catch (FAO & ICES 2008), or about 200% of the 2007 commercial landings (FAO & ICES 2009). In the German lowlands the consumption by cormarants has been estimated amounting 77 t corresponding to 1 kg ha^{-1} annually (Brämick & Fladung 2006).

However, despite considerable conflicts with fisheries managers (Cowx 2003), predation by birds was commonly considered of moderate or minor impact on eel stocks compared to fisheries mortality (Zydelis & Kontautas 2008, Carpentier et al. 2009).

2.2.7. Silver eel migration

In the sea, assessing the spawner stock and natural mortality of migrating silver eels face similar uncertainties like those of leptocephali. Indeed, the potential success of a migratory silver eel reaching the Sargasso Sea has been derived from combining studies of swimming speed (van den Thillart et al. 2004), swimming efficiency (van Ginneken et al. 2005a), energy requirements for swimming and spawning (van Ginneken & van den Thillart 2000, van Ginneken & Maes 2005), and the average energy content of migratory specimen (van Ginneken & van den Thillart 2000). Eels swim four to six times more efficiently than non-eel-like fish (van Ginneken et al. 2005a). In flow tank experiments average costs of travel of 0.42-0.62 kJ kg^{-1} km^{-1} have been determined for eels swimming 5500 km in six month (van Ginneken et al. 2005a). Large silver eel females will use about 40% of their initial fat storage for the 6000 km migration to the Sargasso Sea and remain 60% for gonad development; for a 2 kg silver eel with 20% fat initial content this corresponds to 413 g of eggs and a gonad-somatotrophic index of 22 (van Ginneken & van den Thillart 2000). Fat contents well above 20% total body weight were commonly considered as sufficient for successful spawning (e.g., Svedäng & Wickström 1997, Belpaire et al. 2009). In contrast to Kettle et al. (2008) and Belpaire et al. (2009), who speculated that the smaller male spawner have to recruit from the south-western edge of the distribution area to reach the Sargasso Sea, also male eels from the northern range of the distribution area contain sufficient energy stores for the transatlantic migration and gonad development (van Ginneken & van den Thillart 2000, van den Thillart et al. 2004, 2007, Palstra et al. 2007). However, the contribution of the northern areas to the spawning stock – males and females – may be naturally lower, if they receive only the more or less accidental dispersers, while the vast majority of the progeny approaches at the Biscay (Dekker 2000).

3. Potential management measures

The European eel recovery plan (EC 1100/2007) considers the following measures to enhance the eel spawner stock: reducing commercial and recreational fisheries, improving habitats and longitudinal connectivity, stocking, translocating silver eels to waters with unlimited access to the sea, measures against animal predators, temporary hydropower turbine shut-off, and measures related to aquaculture. Precautionary eel management generally agreed to immediately start with applicable stock rehabilitation measures, even if the primary causalities in eel decline remain uncertain (Feunteun 2002, Russell & Potter 2003, Dekker 2008, FAO &

ICES 2009, ICES 2009). However, independently whether or not all potential influences can be addressed by management measures, also the remaining subset of applicable, reasonable approaches should be prioritized according to their potential efficiency.

There is a generally high uncertainty about the real catches of glass, yellow, and silver eel, resulting from unreliable landing statistics, widely unrecorded catches from recreational and other non-commercial fisheries, but also from poaching. Embedded in the urgent need for more reliable eel monitoring data, fisheries manager have two major options to enhance the eel population: stocking and fisheries restrictions (limited access, bag limits, minimum size limits, temporary or permanent closures). Closures of the glass eel fisheries for varying periods as well as stricter licence controls were found to increase glass eel escapement between 0% and 13% (Beaulaton & Briand 2007). In contrast, even a total closure of eel fishery was expected to result in a full stock recovery not before about 80 years, while just reducing fishery to only 10% of its current level would extend this period to about 200 years (Åström & Dekker 2007) indicating the temporal scale of the eel management. In view of the various significant economic impacts of major eel fisheries closures (Acheson 1981, Knösche et al 2004) combined with its low expected efficiency (Åström & Dekker 2007); substantial closures of eel fisheries seem not an option for stock recovery.

One of the pressures outside fisheries causing significant eel mortality is hydropower use and water abstraction. Downstream migrating silver eels typically follow the main flow, which commonly runs through the turbines (Bruijs & Durif 2009). Although eels are often able to stop and to seek alternative routes (Jansen et al. 2007), they may interrupt or cancel their spawning migration respectively pass through the trash racks, if alternative routes are unavailable or untraceable (Bruijs & Durif 2009). There are several options available to reduce injuries and mortality of downstream migrating fish at hydropower stations, water abstractions, and large dams, from temporary turbine shut-off to fish behavioral barriers, physical barriers like bar racks and fixed screens, fish-diversion devices like drum screens, and fish-collection devices (Clay 1995, ATV-DVWK 2005, Dumont et al. 2005). Most of them have high initial costs and nearly all high operational and maintenance costs (Clay 1995). The efficiency of fish-diversion devices, fish deflectors and bypass facilities depends on the screen's angle to the main flow direction, the flow velocity, and the minimum distance between racks respectively size of screen openings (ATV-DVWK 2005). Unfortunately everything improving the fish protection goes at the expense of power generation efficiency.

However, if fish protection is a generally agreed objective, which has been institutionalized with the implementations of the European eel recovery plan (EC 1100/2007) and the Water Framework Directive (2000/60/EC), such costs and losses have to be essentially considered in pre-investment analyses and economic feasibility studies of barrier constructions for any reason. Similar to car manufacturers having been obliged to equip all vehicles with catalytic converter to meet the standards, artificial barriers have to be equipped with suitable up- and downstream migration facilities for fish.

McCarthy et al. (2008) reported effective increase of silver eel escapement rates by trapping migrating eels at fishing weirs located up-stream of the power station and transporting them towards the estuary. However, all measures demanding permanent operation seem not sustainable and will be immediately canceled if necessary resources and costs are otherwise dedicated.

Equipping weirs and barrages with efficient migration facilities would also improve the natural immigration of eel recruits (Bult & Dekker 2007) and further serve rehabilitating aquatic diversity in general, as prerequisite to restore longitudinal connectivity for river fish assemblages (e.g. Pavlov 1989, Clay 1995, Dumont et al. 2005). However, in large parts of its present distribution area eel depends on stocking (FEUNTEUN 2002, KNÖSCHE et al. 2004, DEKKER 2008, FAO & ICES 2009).

Stocking with glass eel is inversely related to the expanding eel production in aquaculture. It has strongly decreased since the early 1990s and now reached a very low level with a still decreasing trend (ICES 2009): from a total of 33 t glass eels (0.01-0.14 kg ha^{-1} $year^{-1}$) stocked in European waters (FEUNTEUN 2002) it has dropped to 4.5-7.5 t in 2007 (FAO & ICES 2009). At present, FAO & ICES (2009) estimated 7.5-15% of the glass eel catch used for stocking, either directly or as on-grown eels, while in contrast, BRIAND et al. (2008) mentioned only 2% of glass eel used for restocking. The difference to the proportion given by FAO & ICES (2009) might indicate the amount of on-grown eels commonly counted as glass eel equivalents. Glass eel stocking has been increasingly replaced by stocking of larger eels, however, there is some evidence emerged that farmed eels are not performing as well as wild eel (ICES 2009). In aquaculture facilities, eels are further at risk of virus infections with the mentioned lethal consequences for the migratory stage (VAN GINNEKEN et al. 2005b).

The European eel regulation (EC 1100/2007) requires that fisheries make at least 35% of eels <12 cm available for stocking in 2009, rising to 60% by 2013. However, based on the 50-60 t glass eel catch in 2007, even this amount will be less than the required 150-1000 t to supply the whole potential productive habitat (FAO & ICES 2009). Further, given the high handling mortality in glass eel catch (BRIAND et al. 2009, cited in ICES 2009), the 60% restocking quota would immediately prevent any other use of glass eel, e.g. in aquaculture. Thus, there is an urgent need to lower the handling mortality during catch to fulfill the requirements of regulation EC 1100/2007, for example by prohibiting push nets or by switching back to hand nets to produce high quality stocking material. In addition, the recent listing of eel in Appendix II of the Convention on International Trade in Endangered Species of wild fauna and flora (CITES) and its European implementation Appendix B of EG 338/97 (by EG 318/2008) should support saving enough stocking material for the European eel catchments and preventing glass eel exports outside the EU.

Interestingly, it has not been resolved yet whether or not the freshwater eel catchments contribute to eel recruitment and if increasing the escapement rather than stocking rate of glass eel would be most promising to enhance the silver eel spawning stock. For the first time WESTIN (1990) has questioned successful spawning migrations in stocked freshwater eels, because of the observed deficits in olfactory imprints and orientation cues WESTIN 1990, 1998). TSUKAMOTO et al. (1998) stated that catadromous forms of freshwater eels in general do not migrate to the spawning grounds and therefore, do not contribute to maintenance of the overall population. However, this study provided in particular evidence that not all eels show the classical catadromous life cycle and that a certain, largely unknown proportion remains in the marine environment. Observations of 15-23% successfully downstream migrating eels in the Rhine River (KLEIN BRETELER et al. 2007) do not per se contradict the stated primary contribution of the marine eel populations to future recruitment (WESTIN 1990, 1998, 2003, TSUKAMOTO et al. 1998), but show that both life histories may end in migration. LIMBURG et al. (2003) reported that 24% of 36 silver eels caught during emigration from the Baltic Sea had spent at least some time in freshwaters, although 69% of the emigrating silver eels showed no evidence of freshwater residency (LIMBURG et al. 2003). Rather low contributions of 20% and 2% stocked eel have been reported from samples in the Curonian Lagoon and Baltic coastal waters, respectively (SHIAO et al. 2006).

WESTIN (2003) performed a migration study using silver eels stocked as elvers in freshwaters and silvered therein. From 128 recaptures between 3-120 month after release 90% showed surprisingly low fat contents and 63.4% lost weight, leading to the final conclusion that stocked eels lack imprinting and do not contribute to recruitment (Westin 2003). Based on energy requirements for migration proposed by van Ginneken & van den Thillart (2000), catadromous eels were calculated having the highest migration potential (mean = 7149 km), while stocked eels spending their lives in freshwater were supposed to maintain on average only 4938 km – not enough to reach their spawning grounds (Limburg et al. 2003).

The contribution of both life histories to the spawner stock needs further intensive studies, especially if it becomes mixed with potential effects of lacking imprints related to stocking (Westin 1990, 1998). While most freshwater systems depend on eel stocking – often via the bypass aquaculture – no stocking occurs in the marine environment. Thus, the comparison between both life histories so far is in principle a comparison between stocked and naturally recruiting eel with the latter unsurprisingly better performing.

In addition, eels staying in a purely marine environment are at little risk of getting infected with *Anguillicola crassus* (Jakob et al. 2009) or pathological viruses (Hanel 2009, cited in ICES 2009). In conclusion, the common practice of catching glass eel in estuaries for restocking of freshwater systems might therefore even worsen the problem by further diluting the number of eels that would remain in marine habitats (Hanel 2009, cited in ICES 2009).

4. Conclusions

Of the various causes potentially contributing to eel decline, some remain simply unknown especially in the marine life stage, others can not at all (climatic factors) or hardly (pollutants, parasites) be managed, and those seemingly manageable are of uncertain outcome and efficiency (stocking, closures, catch limits). Without doubt, up- and downstream longitudinal connectivity for fish is a practicable as well as efficient measure to enable migrating fish the colonization and use of available habitat patches. It's a rather basic, highly important measure and essential prerequisite to achieve environmental objectives for the whole fish assemblage according to various legislations. The specific improvement of the eel spawner stock is not known and strongly depends on the general contribution of the freshwater habitats to eel recruitment. In freshwaters, eels face a higher risk of infections by parasites and viruses and they often accumulate higher rates of contaminants, organic pollutants and toxins due to the concentrated uses in the catchments. All these factors affect the swimming performance and/or reproductive output of eel, and thus, even surviving, successfully silvering and downstream migrating freshwater grown eels will probably fail to reproduce and to contribute to the stock recruitment (van Ginneken et al. 2005b, 2009, Palstra et al. 2006, 2007, Geeraerts & Belpaire. 2010). Therefore, the contribution of freshwaters to the global eel population may be lower than expected.

Urgent research needs with significant relevance to the European eel management have been identified in determining the relative contribution of freshwater grown eels to the spawner stock, i.e. of catadromous and non-catadromous life histories, respectively of stocked and naturally recruiting eels. This includes investigating what determines the natural colonization of freshwaters by eels and their contribution to the demography of the spawner stock, e.g. to the sex ratio, but also whether or not the reported low performance in catadromous eels primarily resulted from a lack in migratory cues due to stocking. However, if eel spawners primarily recruit from the marine coastal habitats the management in the designated eel catchments may be of minor effect. Than, the stocking material used in freshwaters would represent a net loss for the future spawner generation, in addition to the dramatic handling losses to yield it.

If catadromous eels substantially contribute to the spawner stock or its demography even the management in the designated eel catchments will show effects but the stocking practice should be adapted to avoid imprint failures. Both the performance of stocking material and the contribution of different life histories to the spawner stock need further scientific confirmation. However, given a superior performance of natural recruits, the escape rate of glass eel should be increased expecting that higher numbers approach their natural growth habitats, marine and freshwater. In case of scientific confirmation, regulation EC 1100/2007 should be adapted to increase the glass eel escapement rather than stocking. The latter should be kept at a level sustaining the existing fisheries because of their cultural and economic value, and because even the complete closure of all fisheries was projected to recover the eel stock in about 80 years.

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