

Factors challenging the  
European Eel (*Anguilla anguilla*) stock recovery in  
continental waters

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Erster Gutachter:	PD Dr. Reinhold Hanel
Zweiter Gutachter:	Prof. Dr. Thorsten Reusch
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Für Wiebi, Tine und Hamu

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## ZUSAMMENFASSUNG

Der Bestand des Europäischen Aals (*Anguilla anguilla*) befindet sich seit Jahrzehnten im Abwärtstrend und Bemühungen diesen Trend abzuschwächen müssen bisher als wenig erfolgreich eingestuft werden. Managementmaßnahmen zur Unterstützung der Bestandserholung werden durch die noch immer existierenden Lücken im Wissen um die Biologie der Art und den (vermutlich) panmiktischen Bestand extrem erschwert. Als Reaktion auf die dramatische Bestandssituation sah sich die Europäische Kommission im Jahr 2007 gezwungen zu handeln. Mit Verabschiedung der EG-Verordnung Nr. 1100/2007 wurden europaweite Maßnahmen zur Wiederauffüllung des Bestandes des Europäischen Aals in Kraft gesetzt. Diese verlangen von allen EU Mitgliedstaaten (u.a.) die Sicherung einer Mindestabwanderung von 40% der Blankaalen, gemessen am Zustand ohne anthropogene Einflüsse. Um dies zu gewährleisten wurden alle EU-Mitgliedstaaten aufgefordert, Aalbewirtschaftungspläne auf Ebene der relevanten Flusseinzugsgebiete einzureichen. Im Rahmen der Erstellung der deutschen Aalbewirtschaftungspläne wurde deutlich, dass die Berechnung der Referenzabwanderung (ohne anthropogene Einflüsse) sowie die direkte Erfassung der momentanen Blankaalabwanderung kaum möglich und die Berechnung der Mindestabwanderung somit auf zahlreichen Vermutungen basieren muss. Aus demselben Grund erweist sich die Beurteilung der bisher getroffenen Managementmaßnahmen zur Auffüllung des Aalbestandes auf nationaler und europäischer Ebene als extrem schwierig.

In der vorliegenden Arbeit konnte erstmals die gesamte Blankaalabwanderung eines mittelgroßen Binnengewässers (Schwentine Flusssystem) in Norddeutschland über einen Zeitraum von 3 Jahren direkt erfasst werden (**Kapitel I**). Die seltene Möglichkeit die komplette Abwanderung von adulten Aalen, sowie die Rekrutierung von Jungtieren (durch Besatz) direkt zu erfassen und nicht abschätzen zu müssen, sowie die Quantifizierung verschiedenster Sterblichkeitsfaktoren für Aale im untersuchten Binnengewässer, ermöglichte die Dokumentation der Einflussfaktoren auf die Anzahl der abwandernden Blankaale. Hierdurch war es möglich, die Blankaalproduktion des Schwentinesystems zu beurteilen und die erfasste Abwanderung mit den Vorgaben der EG-Verordnung, bzw. der Aalbewirtschaftungspläne, zu vergleichen. Dabei wurde deutlich, dass bisherige Abschätzungen der Blankaalproduktion des Schwentine Systems die tatsächlich stattfindende Abwanderung offensichtlich überschätzen. Dies kann weitreichende Folgen für die weitere Entwicklung des Aalbestandes haben, führt die Überschätzung der Abwanderung doch zur fehlerhaften Beurteilung bereits etablierter Managementmaßnahmen.

Da die Möglichkeit die Blankaalabwanderung direkt zu erfassen in der Regel nicht gegeben ist, sind Wissenschaftler in ganz Europa darauf angewiesen, die tatsächliche Abwanderung mit Hilfe von Populationsmodel zu schätzen. Um die Genauigkeit solcher Modellierungen zu beurteilen, ist es dringend nötig die Realitätsnähe der Modelle zu evaluieren. Die Modelsergebnisse mit der tatsächlich dokumentierten Abwanderung vergleichen zu können, schafft hier für nahezu ideale Bedingungen. In **Kapitel II** wurde das in den deutschen Aalbewirtschaftungsplänen verwendete German Eel Model II (GEM II) genutzt um die potentielle Blankaalabwanderung der Schwentine zu modellieren. Hierfür war es zunächst nötig, dass Modell an die systemspezifischen Charakteristika der Aalpopulation der Schwentine anzupassen. Die mit Hilfe des angepassten GEM II geschätzte potentielle Blankaalabwanderung entsprach in etwa der tatsächlich dokumentierten Abwanderung (**Kapitel I**). Die Ergebnisse dokumentieren das enorme Potential des GEM II. Gleichzeitig verdeutlichen sie aber auch die Notwendigkeit der Erfassung systemspezifischer Populationscharakteristika um die höchstmögliche Realitätsnähe des Modells zu gewährleisten.

Bisher beschränken sich die Maßnahmen zu Wiederauffüllung des Aalbestandes in erster Linie auf die europäischen Binnengewässer. Um die geforderten Mindestabwanderungen zu sichern, konzentrieren sich viele EU Mitgliedstaaten unter anderem darauf, bestehende Besatzprogramme auszubauen. Dafür werden schon jetzt große Mengen Glassaale an den Küsten von Frankreich und Spanien gefangen und auf Binnengewässer in ganz Europa verteilt. Diese Praxis ist nicht unumstritten, konnte doch bisher nicht endgültig geklärt werden, inwiefern sich der Transport von Glassaalen aus dem Atlantik nach Nordeuropa auf deren Fähigkeit die richtigen Wanderouten zum Laichgebiet zu finden auswirkt. Deshalb wurden für **Kapitel III** Blankaale aus dem Schwentine System mit externen „T-Bar Anchor Tags“ markiert und dann erneut in die Schwentine gesetzt um eine ungehinderte Abwanderung zu ermöglichen. Wiederfangmeldungen konzentrierten sich in der dänischen Beltsee. Die Ergebnisse lassen darauf schließen, dass besetzte Aale trotz des Mangels eines imprintings der Wanderroute in der Lage sind, den Weg aus der Ostsee zu finden. Gleichzeitig konnte jedoch auch gezeigt werden, dass die Wandergeschwindigkeiten der besetzten Aale deutlich zu langsam sind, um rechtzeitig im Laichgebiet anzukommen. Es scheint, als würden die Aale nach der richtigen Route suchen müssen und wären somit nur bedingt in der Lage ohne imprinting zielgerichtet abzuwandern. Es muss deshalb in Frage gestellt werden, ob diese besetzten Aale noch Teil der effektiven Population sind und somit zur Arterhaltung beitragen können.

## SUMMARY

The European eel (*Anguilla anguilla*) stock has been in a steep decline for the last decades. So far, established management measures to impel stock recovery have to be considered of only minor success. Still existing questions about the biology of this facultative catadromous and presumably panmictic species further complicate both the evaluation of current management decisions and the implementation of additional management measures. As a reaction to the dramatic development of the stock, the European Commission issued EU Regulation No. 1100/2007. Thereby, all Member States are asked to secure a minimum escapement goal of 40% of escaping silver eels with respect to a pristine state without any anthropogenic influences. To document the current state of national eel stocks and describe the planned conservation activities, Member States were asked to prepare so-called Eel Management Plans (EMP) for identified eel river basins. While doing so, it became obvious that the direct assessment of escapement numbers is hardly possible and estimates had to be based on a number of assumptions. For the same reason, already established management measures are extremely challenging to be evaluated, both on a national and a European level.

In the present thesis, it was for the first time possible to directly assess the entire silver eel escapement from a medium freshwater system in Northern Germany (Schwentine river system) over a 3-year period (**Chapter I**). The rare possibility to document the complete escapement of silver eels out of the system and the complete recruitment (via stocking) to the system, allowed for the characterization of factors acting on the amount of emigrating spawners. Thereby, it was possible to document the potential of the Schwentine river system to produce (healthy) silver eels and compare the results with the escapement requirements of the EU Regulation. It became obvious that current estimates of the silver eel escapement from a freshwater system in Northern Germany (given in the EMP) are overstated. Such an overestimation will have severe consequences for the future development of the European eel stock, because it might lead to a false-positive evaluation of the management success.

As it is usually not possible to directly assess the entire silver eel escapement from a freshwater system, scientists across Europe rely on population dynamics models to describe the spawner output. To evaluate the accuracy of such model-approaches, it is of high importance to assess how close to reality the model output actually is. Comparing modeled escapement numbers with the directly assessed *in situ* silver eel output provides possibly the best evaluation of the model



potential. In **Chapter II**, the German Eel Model II (GEM II), applied in the German EMP, was used to estimate the potential silver eel output of the Schwentine river system. To do so, it was first necessary to adjust the GEM II for the system-specific population characteristics of the Schwentine river eel population. Estimated escapement numbers were in the same range of the actually documented escapement in **Chapter I**. Results, thereby, document the potential of the GEM II in providing the necessary base for sound management decisions. At the same time, however, **Chapter II** illustrates the absolute necessity to minimize the generalization of input parameters. Only by a fine adjustment of input parameters to system-specific population characteristics, it is achievable to ensure the highest model accuracy possible.

Up to date, management of the European eel is primarily restricted to the inland waters of the European Member States. In order to fulfill the required minimal escapement numbers, many Member States decided to extend already existing stocking programs. Today, these programs already require huge numbers of glass eels, caught at the coast of France and Spain and then allocated all across Europe. This procedure is subject of a lot of controversy, because it is still not entirely clear, whether the translocation of glass eels from the Atlantic coast to Northern Europe interferes with their ability to find the spawning location once they become silver eels and leave continental inland waters. Therefore, in **Chapter III**, formerly stocked silver eels from the Schwentine river system were tagged with T-Bar Anchor Tags to track their migration route through the Baltic Sea and evaluate their migratory success. Recapture reports accumulated in the Danish Belt Sea and results indicate the capability of stocked eels to successfully find the passage from the Baltic Sea into the North Sea without being dependent on an imprinting. In addition, however, documented migration speeds had to be considered to be too slow to reach the spawning ground in time for reproduction. The lack of imprinting seems to force the eels to search for the right route and it is highly questionable whether these eels are still part of the effective population size and thus can contribute to the stock recovery.

## GENERAL INTRODUCTION

### Origin of the genus *Anguilla*

There are more than 800 species of eels described in the order of Anguilliformes (Inoue et al. 2010). Within this extraordinary divers order only 18 recognized species (including three subspecies) are able to inhabit freshwater systems at some part of their life (Inoue et al. 2010). These “freshwater eels” constitute the genus *Anguilla* (family Anguillidae, first described by Schrank in 1798) and are found in a number of different habitats all over the world (Tesch 1999; Lecomte-Finiger 2003). Out of the 18 recognized species, *Anguilla celebesensis* has been thought to be one of the possible ancestral species. *A. celebesensis* mainly inhabits Sulawesi Island (Celebes), Indonesia, suggesting the tropical western Pacific as the place of origin for freshwater eels (Aoyama and Tsukamoto 1997). With the breakup of Pangaea (24-36 million years ago) westward circum-equatorial current through the Tethys Ocean may have led to the dispersal of ancestral anguillid eels to what is today the Atlantic Ocean. The two anguillid eel species found in the Atlantic today, the European eel (*Anguilla anguilla*) and the American eel (*Anguilla rostrata*) most likely separated about 10 million years ago (Lecomte-Finiger 2003). Lin et al. (2001), however, contradicted this hypothesis by sequencing cytochrome b and 12S rRNA. They estimated an approximate age of the genus *Anguilla* of 20 million years. Under such suggestions, the idea of ancestral anguillid eels dispersing through the Tethys has to be dismissed as it was already closed by then and the only possible dispersal route of the Atlantic eels would have been the American gateway between North and South America (Lin et al. 2001). The question of the geographic and phylogenetic origin of the Atlantic eels is only one of still numerous mysteries surrounding the genus *Anguilla*.

Distribution patterns of this genus are strongly connected to the unusual life-cycle of its members. Freshwater eels are catadromous, semelparous fish with fully marine spawning grounds in the world oceans and prolonged growing phases in continental brackish and freshwater habitats (Tesch 1999). Their distribution throughout the world appears to be strongly connected to the subtropical circulations of the oceans. As a result of westward-flowing equatorial currents freshwater eels are primarily found on the east coasts of Eurasia, Australia, Africa and North America (Aoyama and Tsukamoto 1997). In the North Atlantic, however, the warm eastward-flowing Gulfstream and North Atlantic drift sustain the only anguillid eel species found on a continental west coast - the European eel, *Anguilla anguilla* (Aoyama and Tsukamoto 1997).

## The European eel (*Anguilla anguilla*)

The European eel is a semelparous, facultative catadromous fish species populating marine and freshwater habitats all over Europe and northern Africa. Its distribution ranges from the Scandinavian coast down to Morocco (Dekker 2003b). Despite over one hundred years of intensive research, there are still numerous unsolved questions about the biology of *A. anguilla*. Even though the Sargasso Sea (23-30°N 48-74°W) is commonly considered to be the spawning ground of both, the European and the American eel, the proof still needs to be given. Up to date, not a single eel has ever been caught in the open Atlantic Ocean, respectively the suggested spawning ground. However, scientific catches of eel larvae (leptocephali) in the open ocean were already reported at the beginning of the last century by Johannes Schmidt (1923). He was able to catch leptocephali with less than 10mm in size and was the first to suggest the Northwest Atlantic as the spawning ground of the Atlantic anguillid eels (Figure Intro-1). Today, the location of the spawning site is no longer questioned.

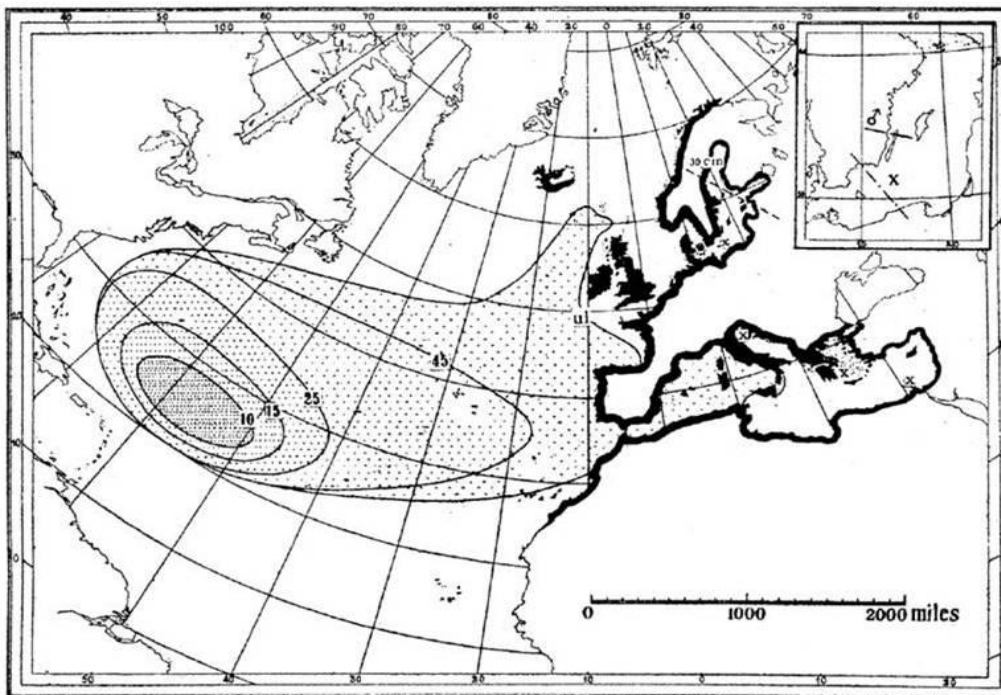


FIGURE INTRO-1 Distribution of European eel (*Anguilla anguilla*) larvae with respective length. Black coastline indicates distribution of the species along Europe and North Africa. Source: Schmidt (1923). Figure taken from van Ginneken & Maes (2005)

Originally, the **lifecycle** of *the* anguillid eels was thought to be clearly separated into a marine spawning and larval phase and a prolonged continental freshwater growth phase, as depicted in Figure Intro-2.

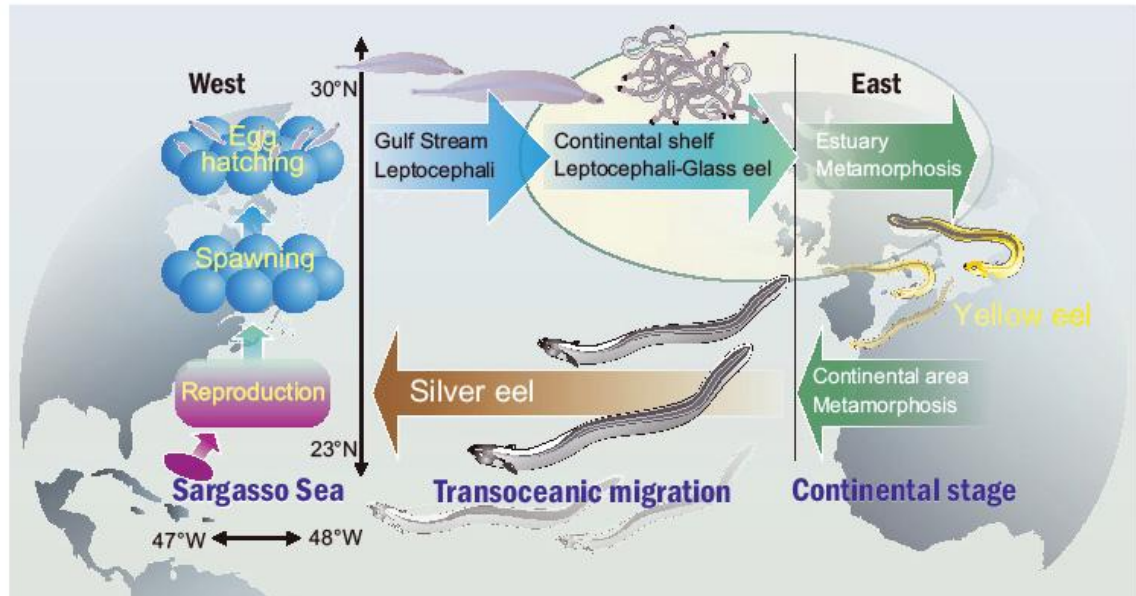


FIGURE INTRO-2 lifecycle of the European eel (*Anguilla anguilla*). Source: Bru et al. (2009)

Tsukamoto et al. (1998) challenged this classical view by showing that significant numbers of *Anguilla japonica*, the Japanese eel, and *Anguilla anguilla* do not migrate into freshwater but rather spend their whole life in marine and brackish coastal waters. The same was shown for *Anguilla rostrata*, the American eel (Daverat et al. 2006; Thibault et al. 2007). Nowadays, the classical view of a clear separation between a marine and a freshwater phase is rejected for the European eel and instead the species is considered to be facultative catadromous. During their continental phase, some specimens migrate between freshwater and marine habitats, while others even spend their whole growth phase in marine coastal waters. This process is probably driven by eel density and/or habitat quality (Briand et al. 2005; Bevacqua et al. 2011). Even though there are still numerous questions about some particular details, the main parts of the simplified lifecycle in Figure Intro-2 hold true.

The lifecycle of the European eel is characterized by **two long-distance migrations** (5000-7000 km) across the Atlantic Ocean. The first one occurs following hatch when the **leptocephali** are transported by the eastward-flowing Gulfstream and the North Atlantic Drift towards the European continent. There has been some discussion about the duration of this drift, with estimates varying between 6 months and a few years. Obviously, duration of larval

migration/transport depends on whether the leptocephali are capable of active, target-orientated swimming (Lecomte-Finiger 1992; Lecomte-Finiger 1994) or rather completely dependent on the Atlantic current systems (Bonhommeau et al. 2009). Based on growth history and age at recruitment of European glass eels, Lecomte-Finiger (1992) estimated the duration to be only 6 to 9 month. Bonhommeau et al. (2009) assumed no active swimming and used a Lagrangian particle drift model to estimate the minimum duration of a passive leptocephali transport over the Atlantic Ocean. They concluded that a passive transport of eel larvae across the Atlantic Ocean to the European coast would take about 10 months. In contrast, comparing glass eel recruitment with oceanic oscillations, Knights (2003) suggested a 2.5 to 3 yr period.

Upon arrival in European continental waters the leaf-like leptocephali metamorphose into the so-called **glass eels**. Subsequently, the non-pigmented glass eels start their immigration into estuaries and freshwater systems and become pigmented elvers (Figure Intro-2). The duration of the following growth phase in continental coastal and freshwater habitats, during which the eels are now called **yellow eels**, differs between sexes and is highly variable among subpopulations all over Europe (Vøllestad 1992; Davey and Jellyman 2005). While males usually do not spend more than 6-9 yrs in continental waters before leaving to reproduce, female **continental residence** can exceed 20 yrs (Tesch 2003). This difference is thought to be the result of **sex specific reproductive strategies** (Tesch 2003; van Ginneken and Maes 2005). Male reproductive success is most likely rather dependent on the ability to reach the spawning grounds than body size, while female fecundity highly depends on body size and energy reserves for maturation and spawning (Vøllestad 1992; Davey and Jellyman 2005; Palstra and van den Thillart 2010). It has been shown that mean age-at-metamorphosis and thus the **duration of the continental phase** is highly correlated between sexes and both females and males mature younger in populations of high growth rates (Vøllestad 1992). Vøllestad (1992) suggested that the negative correlation between mean age at the silver stage and the mean growth rate is not only governed by local environmental factors but could also be explained by the duration of the larval drift. This suggestion was based on observed correlations between length at maturity and latitude as well as distance to spawning area. Svedäng et al. showed that mean age of female silver eels in Sweden ranged from 12 to 19 yrs (1996). He documented that the duration of the continental growths phase is highly depending on food-availability and habitat quality (Svedäng et al. 1996) and further suggested that reproductive strategy in female *A.anguilla* is to “become sexually mature at the earliest possible opportunity” and thereby contradicted previous hypothesis where female reproductive tactic favors size-maximizing over time-minimizing (Larsson et al.

1990; Vøllestad 1992). The cost associated to the increased risk of pre-mature mortality during prolonged continental residence seems to be balanced by the increase in fecundity with size and thus maximizing size at maturity seems to be the optimal strategy for females (Davey and Jellyman 2005).

Glass eels enter continental freshwater as sexually undifferentiated juveniles and sex determination in the Atlantic eels is believed to be environmentally induced (Wiberg 1983; Davey and Jellyman 2005). Hereby, northern habitats often seem to promote the development of female-dominated subpopulations, while southern European habitats often support complete male dominance (Tesch 2003). These differences are thought to be the result of varying habitat quality and population densities with high temperatures and densities biasing the sex ratio towards males (Krueger and Oliveira 1999). Holmgren and Mosegaard (1996) showed that differences in early growth influences the future sex of undifferentiated eels, with small males growing faster in weight than females. They conclude that *“an undifferentiated individual that grows fast in weight might benefit in fitness by becoming a male and mature at low age and size [and] a potential female that grows slower [...] might later on compensate its higher age with increased fecundity”*. By using mathematical modeling, Melia et al. (2006) were able to show that a critical size (rather than age) seems to be a trigger for sex differentiation. They compared different habitats and documented that while the age-at-differentiation varied between the habitats, length-at-differentiation was almost constant (Melia et al. 2006). Additionally, females in all habitats grew faster than males. Melia et al. (2006) thereby contradicted Holmgren and Mosegaard (1996), but supported several previous investigations looking at the sexual differentiation in eels (Vøllestad 1992; Panfili et al. 1994; Poole and Reynolds 1996). With the constant increase in stocking and the (intensive) exploitation of subpopulations all over Europe, densities in eel habitats are heavily influenced by anthropogenic interactions (Wickström et al. 1996; ICES 2010a; Acou et al. 2011; Pratt and Threader 2011). Wickström et al. (1996) documented that stocking may also have significant influence on the sex ratio of subpopulations. Despite high stocking numbers, only approximately 3.4% of stocked glass eels developed to males (Wickström et al. 1996).

The ***end of the continental growths phase*** is marked by a fourth metamorphosis (Figure Intro-2). In order to prepare for the final long-distance oceanic migration to the spawning ground premature yellow eels of both sexes get enlarged eyes and fins as well as undergo a color-change and are then called “silver eels” (Pankhurst 1982; Tesch 1999). These silver eels cease feeding which is accompanied by the reduction of the digestive tract and usually start their

migration in autumn (Pankhurst and Lythgoe 1982; Tesch 2003). In general, the emigration of silver eels from freshwaters across Europe starts in fall. It has been reported that males tend to start the migration earlier than females. The **onset of the emigration** from continental inland waters has previously been linked to dark new moon nights with high water discharge (Durif et al. 2008a,b). However, several authors were not able to support these findings and triggers remain poorly understood (Breukelaar et al. 2009; Tsukamoto 2009). Nevertheless, scientists all over the world agree that the onset of the spawning migration most likely is triggered by a combination of physiological condition, behavioral drive and eventually environmental factors (Vøllestad et al. 1986; Tsukamoto 2009).

Little is known about the **open-ocean spawning migration** of silver eels to the Sargasso Sea (Tsukamoto 2009). Up to date, it is still unclear how migrating silver eels are able to **locate the spawning ground** and assumption range from magnetic orientation over olfactory clues to salinity (Tesch 1970; Westin 1990; van Ginneken et al. 2005b; Tsukamoto 2009). In general, diadromous fishes are expected to imprint the migration route to the natal side on their larval migration (Leggett 1977; Hansen et al. 1993; Dittman and Quinn 1996). If this holds true for the European eel, the translocation of juvenile eels might impair their ability to find the spawning ground and these individuals would eventually be lost from the effective population size. Even though it has been shown that at least in some cases, homing behavior in European eel after small-scale translocation is strikingly effective (Tesch 1970), little is known on how large-scale translocation (stocking in Northern Europe with glass eels originating from the Bay of Biscay) affect the spawning migration. So far, scientific studies draw a mixed picture of the influence of stocking on migratory success with some studies highly questioning the contribution of stocked individuals to the spawning stock (Westin 1998; Westerberg et al. 2007).

While the timing/onset of the migration is easily assessable, the open-ocean migration route still remains a mystery. However, recent technological developments allow equipping large female silver eels with satellite tags (Aarestrup et al. 2009). These tags are externally attached to the dorsal muscle and programmed to pop-up after a given time period. Once the tags reach the ocean surface, they connect to a satellite and send the recorded depth, temperature and (optional) salinity data. Thereby, it was possible to document diurnal diving patterns with eels migrating in warm shallow waters during night (approximately 300 m) and a deeper swimming depth (approximately 600 m) during the day (Aarestrup et al. 2009). So far, the reason for this behavior is subject of broad discussions. Possible reasons range from predator avoidance to metabolic reasons and delaying gonadal development (Aarestrup et al. 2009). Additionally, the results by Aarestrup et al. (2009) suggest a southwesterly migration route towards the Canary

and Azores current system. Silver eels seem to use the south- and west-flowing currents beginning west of Africa to increase their travel efficiency (Aarestrup et al. 2009).

Knowledge about the actual **spawning behavior** of *A. anguilla* in the open ocean is virtually non-existent. So far, almost everything published is based on hormone-induced reproduction of *A. anguilla* and *A. japonica* in captivity (Boëtius and Boëtius 1980; Dou et al. 2007). Up to date, the probably most comprehensive description of induced spawning behavior was given by Van Ginneken et al. (2005c). They documented male-male, female-male and female-female interactions and concluded that spawning in *A. anguilla* most likely is collective and simultaneous (Van Ginneken et al. 2005c). Information about the actual spawning depth is likewise rare. The combination of larval catch data and release experiments in the Sargasso Sea indicates a depth between 50 and 300m (Castonguay and McCleave 1987; van Ginneken and Maes 2005).



## European Eel Fisheries and Status of the Stock

For centuries, the European eel has been an important target species for fishermen all over Europe (Tesch 1999). However, the current stock is considered to be out of safe biological limits and *A. Anguilla* has been listed as “critically endangered” in the “Red List of Threatened Species” by the International Union for Conservation of Nature (Dekker 2003b; Freyhof and Kottelat 2010). Additionally, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listed the species in Appendix II, requiring export permits for exporting countries.

A downward trend in recruitment was first recognized in 1985 (Dekker 2003c). It took, however, until the beginning of the 1990s for its effect on the stock and the fisheries to be considered (Dekker 2003c). By 1997, the spawning stock biomass was still considered to be sufficient to sustain the population (Moriarty and Dekker 1997). Only two years later, in 1999, the stock was then considered to be out of safe biological limits by the ICES Advisory Committee in Fishery Management (ICES 1999). More recent evaluations of time series depict a dramatic picture (Dekker 2003b; ICES 2011a), even though an exact estimate of the population size has been proven to be difficult. Virtually every single time series gathered by the European Inland Fisheries Advisory Committee (EIFAC) depicts a steep decline since the 1980s and time series depicting the yellow eel recruitment are currently at 9% of their mean 1960-1979 levels (Figure Intro-3; (ICES 2010a). Time series documenting the abundance of glass eels in Europe draw a picture even more dramatic. Today, glass eel abundance averages between 1% (continental North Sea) and 7% (elsewhere in Europe) of 1960-1970 levels (ICES 2010a).

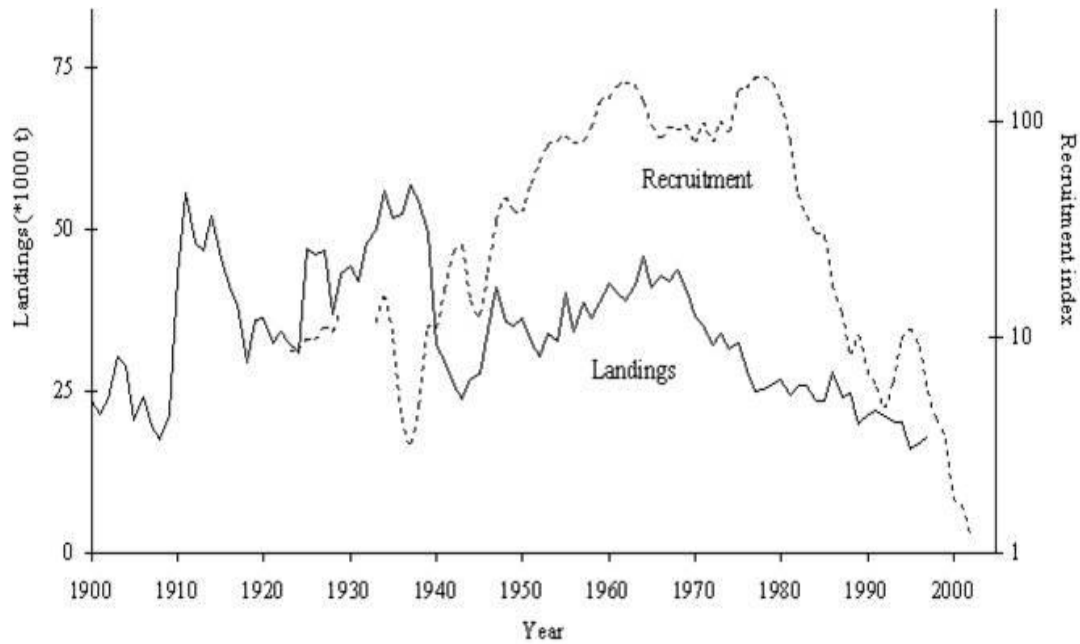
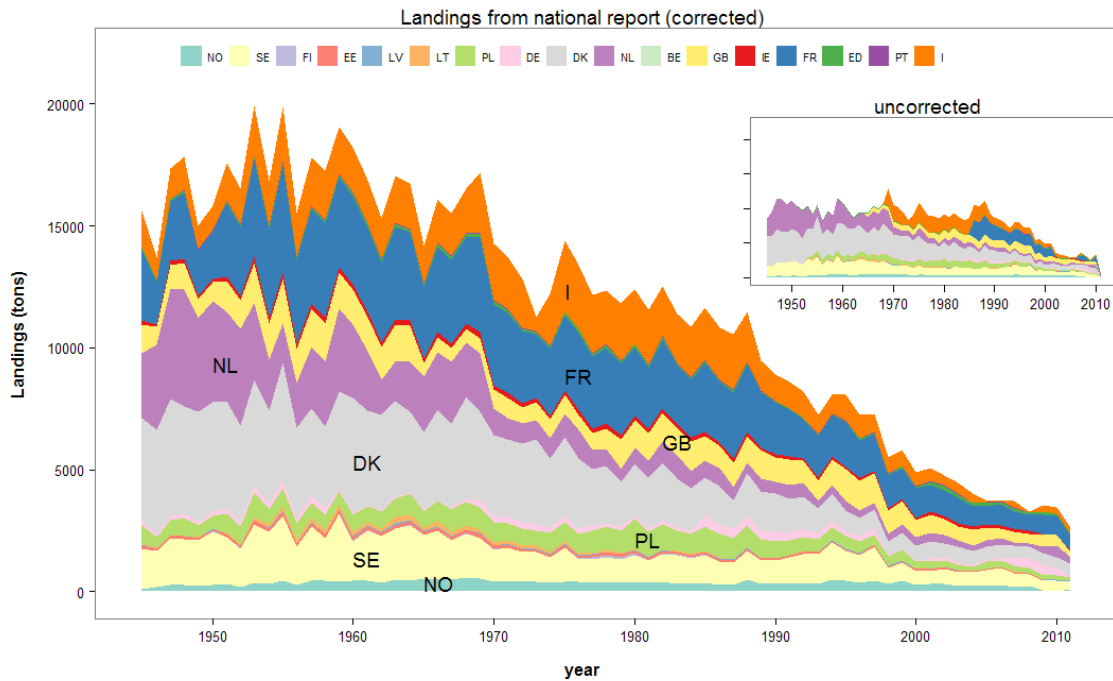


FIGURE INTRO-3 Estimated trends in landings and recruitment of *A. anguilla*. Source: ICES, [www.ices.dk/marineworld/eel.asp](http://www.ices.dk/marineworld/eel.asp)

In general, Moriarty and Dekker described the eel fishing industry to be small-sized and scattered all over Europe with local stock density controlling what life stages are targeted (Moriarty and Dekker 1997; Dekker 2003b).

High stock densities in the centre of the distribution range support a predominance of glass eel fisheries (Dekker 2003b). **Glass eel fishery** throughout Europe is carried out in over 90 estuaries but varies between and within countries. Up to 87% of total European glass eel catches are reported from the Bay of Biscay with the most intensive fishery being located in France (Moriarty and Dekker 1997; Dekker 2000). Estimating the total yield of the European glass eel fishery is challenging as the progressing sparsity of the resource is promoting illegal non-reporting of catches (Dekker 2003c). The best estimate of the European-wide glass eel catch in 2011, however, was approximately 41 tonnes with France alone reporting almost 34 tonnes (ICES 2011a).

While the European glass eel fishery is clearly centred around France, **yellow and silver eels** are caught all over the distribution area with the predominance of silver eels in northern catches most likely being “an adaptation of the fisheries to low stock densities”(Dekker 2003b). Similar to the glass eel fishery, data series on total eel landings often remain unreliable (ICES 2011a). The downward trends in recruitment and glass eel time series are, however, also mirrored in landings all over Europe (Figure Intro-4; ICES 2011a).



**FIGURE INTRO-4** Trend in Landings of *A.anguilla* (all life stages) from the available 2011 ICES WGEEL country reports. Corrected Trend has missing data filled in by a Generalised linear Model (GLM). Source: Report of the 2011 Session of the Joint EIFAAC/ICES Working group on eels

A large proportion of the overall eel yield in Europe is coming from **aquaculture**. As it is not yet possible to reproduce the European eel artificially on a commercial scale, aquaculture facilities depend upon the collection of wild-caught juveniles as stocking material (Minegishi et al. 2012). As mentioned above, glass eels caught in the Bay of Biscay are, therefore, often transferred into aquaculture facilities and grown until market size. Global European eel production in aquaculture has been on the rise for decades but is declining since the beginning of the century (Figure Intro-5). This is most likely the result of the increasing sparsity of stocking material and the export ban to countries outside the European Union.

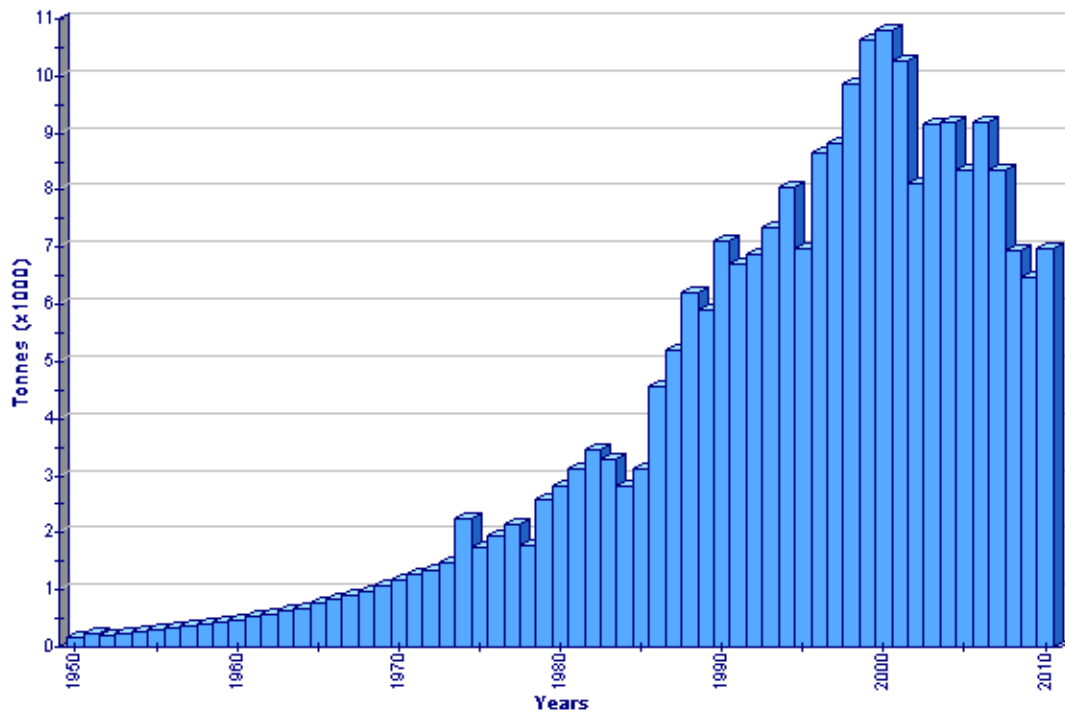


FIGURE INTRO-5 Global aquaculture production of *A. anguilla*. Source: FAO Fishery statistic, Source: [www.fao.org/fishery/culturedspecies/Anguilla\\_anguilla/en](http://www.fao.org/fishery/culturedspecies/Anguilla_anguilla/en)

## Possible Reasons for the Decline

Reasons for the decline are thought to be manifold. Often, factors acting on the European eel stock are broadly grouped into continental and oceanographic causes. They range from anthropogenic influences (e.g. overexploitation and migration barriers) over predation by birds (e.g. cormorants) and reduced spawner quality (parasites and viruses) to oceanic changes due to climate change and act on virtually every stages of the complex life cycle of European eel (ICES 2010a, 2011a).

One of the factors often held responsible for the decline of the *A. anguilla* stock is **overexploitation** in European waters. The eel fishery has great cultural importance with an enormous public perception all over Europe and virtually every life stage of the European eel is harvested (Dekker 2003b).

Upon arrival in continental waters glass eels are caught for direct consumption (Europe and Asia) or stocking (Moriarty and Dekker 1997). The European glass eel fishery concentrates around the Bay of Biscay with approximately 87% of total European glass eel catches being reported from France, Spain and Portugal (Dekker 2000) with fishing season usually lasting from November to April (Briand et al. 2003). Bru et al. (2009) described an average overall exploitation rate of almost 16% in a catchment in southern France. However, rates of exploitation vary a lot and can reach over 90% (Briand et al. 2003). The glass eel fisheries constitutes up to 60% of the overall fishing mortality for all life stages in the Bay of Biscay (Dekker 2000). Glass eels caught at the Atlantic coast, are used for restocking in European waters and direct consumption. A large proportion of European glass eel catches was exported to Asia (Dekker 2003c) until the EU banned all eel exports in 2011. Besides dramatically reducing the glass eels recruitment to freshwater, the glass eel fisheries is often causing extremely high post fishing mortalities of up to 82% within the first two days after catch (Briand et al. 2007).

As there are hardly any glass eels arriving in German coastal waters anymore, main focus of commercial and recreational fishermen in Germany lies on the yellow stage of the European eel (ICES 2011a). Although the yield of the commercial inland eel fisheries in Germany has dropped by approximately 50% within the last 15 years, commercial and recreational catches summed up to around 650 tonnes in 2010 (Anonymous 2012). For the years 2008 -2010, the overall fisheries mortality for the entire German eel stock was calculated to be approximately 1.8% (Anonymous 2012). The vast majority of the overall eel catches is reported from inland waters. However,

especially in the Baltic Sea yellow and silver eels are often targeted by mainly small coastal eel fisheries (Anonymous 2008).

Legal restriction of the eel fisheries are manifold and at the same time often intensively discussed. They differ with federal states and range from restricting the minimal landing size (increase to 45 – 50 cm) and the total yield over regulating fishing gear to closed fishing seasons during the migratory phase of silver eels (ICES 2011a; Anonymous 2012).

Due to anthropogenic interventions eel habitats all over Europe are no longer accessible, degenerated or even completely lost (Feunteun 2002). The introduction of environmental toxins (e.g. PCB and other dioxin-like compounds) into rivers and lakes by industrial processes and the obstruction of dams and hydropower stations were shown to potentially cause high damages and mortalities.

**Migration barriers**, e.g. hydropower stations and dams, have been identified as a major factor in reducing the local stocks of European eel on a catchment level (McCarthy et al. 2008; Laffaille et al. 2009). First, man-made obstacles often constitute insurable barriers for immigrating juvenile eels and affected freshwater systems are often lost as natural eel habitats. Even though glass eels are known to show impressive climbing ability (Imbert et al. 2008) and might therefore be able to pass a variety of migration obstructions, the associated migration-delay most likely increases the predation risk and resulting energy loss may lastingly influence their condition and survival (Mouton et al. 2011). However, river blockage not only affects the amount and condition of immigrating juveniles but also has severe influences on the emigration success of silver eels leaving the freshwater systems on their way to the spawning ground. Turbine passages often cause extremely high size-dependent mortalities in silver eels and have been recognized to be a major threat of local eel populations (Behrmann-Godel and Eckmann 2003; Winter et al. 2007; Calles et al. 2010; Pedersen et al. 2012). The elongated body shape of eels additionally aggravates the high risk of severe injuries that usually entail death. As a result, more and more hydropower stations have been equipped with fish protectors in front of the turbine entries. However, up to date the efficiency of a wide variety of approaches to prevent eels from passing the turbines is still subject of an intensive discussion (Adam 1998; Gosset et al. 2005; Travade 2005; Russon et al. 2010; Hassinger 2011). To reduce the overall mortality of migrating silver eels due to hydropower stations, several catch-and-carry programs are being initiated all over Europe (ICES 2011a; Anonymous 2012). The idea is to catch migrating silver eels (often by commercial fishermen) and transport them pass the hydropower stations to allow for a save migration out of the freshwater systems (Anonymous 2012).

Besides fishing pressure and migration barriers, overall reduction in fitness (primarily energy reserves and parasite infection) of silver eels may pose an additional threat to the maturing individuals and thereby to the entire stock. In 2009, Belpaire et al. showed with the help of two large and independent data sets that the average fat content of yellow eels has decreased by one third over the past 15 years (Belpaire et al. 2009). As the fat content of yellow eels is assumingly indicative of the fat reserves available for silver eels, the over-all decrease may pose an additional severe threat for the reproductive potential of spawners leaving the European coast.

Regardless of an overall improvement of water quality, numerous habitats have still considered to be lost for the production of healthy spawners. Even though long-time series of PCBs (polychlorinated biphenyls) and organochlorine pesticides in European eel show a decrease in contamination (Maes et al. 2008), **environmental toxins** are still considered to be a major threat for eels in European freshwaters (Robinet and Feunteun 2002; ICES 2011a). Hereby, the remobilisation of in fat stores accumulated toxic substances during the spawning migration and the associated loss in spawner quality due to damages in several different organ systems is of primary concern (Palstra et al. 2006; Geeraerts and Belpaire 2010). Levels of contamination with environmental toxins are highly variable with freshwater systems and the high position of eels in European freshwater food webs often predestines them to be used “*as models for the chemical status of rivers*” (Belpaire et al. 2008).

Not only toxins and their remobilisation pose a threat to the successful reproduction of European eel, but also the infestation with **parasites** is thought to reduce the quality of spawners leaving freshwater systems. In the early 1980s, the swimbladder nematode *Anguillicoloides crassus* was introduced to European freshwater systems from Asia by uncontrolled intercontinental transfer of live eels (Kjøie 1991). Today, this blood-sucking parasite is present in almost all inland waters across Europe (Jakob et al. 2009a; ICES 2011a). While *A. crassus* causes hardly any damage in the Asian *Anguilla japonica*, *A. anguilla* becomes heavily infected and resulting pathological changes in the swimbladder (Abdelmonem et al. 2010) presumably reduce the ability to perform documented diurnal diving patterns of silver eels (Kjøie 1991; Clevestam et al. 2011). In general, parasite infections entail defence reaction of the body and will often increase the overall cost of (e.g.) the spawning migration (Clevestam et al. 2011). It has therefore been postulated that high infection rates will result in premature energy

depletion on the long-distance migration and eventually lead to less silver eels reaching the spawning ground or participating in the reproduction event (Clevestam et al. 2011).

Along with parasite infections, there are numerous diseases reducing the spawner quality of silver eels and in some situation leading to direct mortalities. Above all, the the ***Herpesvirus Anguillae*** (HVA) was identified to severely affect local eel populations under certain environmental circumstances. It was first isolated in the 1990s and since then has been documented in numerous different freshwater systems in Germany and Europe (Davidse et al. 1999; van Ginneken et al. 2004; Jakob et al. 2009b; Haenen et al. 2010). Infections can cause severe pathological alterations (e.g. haemorrhages in the skin and fins) and reduce the stress resistance potentially leading to death (Haenen et al. 2002; Hangalapura et al. 2007). Besides HVA there are two more viruses isolated from European eel – ***Eel Virus European X (EVEX)*** and ***Eel Virus European (EVE)*** (van Ginneken et al. 2004). Eels infected with the rhabdovirus EVEX again develop haemorrhages and show a significantly reduced ability to successfully migrate to the spawning grounds (van Ginneken et al. 2005a).

***Predation by the great cormorant (Phalacrocorax carbo)*** has often been condemned to be an additional factor reducing the European eel stock. Indeed, cormorant numbers are increasing all over Europe (Flore and Huppopp 1997; Collas and Burgun 2011) and diet spectrum analysis showed extraordinary diverse prey composition with eels constituting a varying but sometimes significant proportion (Engstrom 2001; Carss and Ekins 2002). However, recent studies seem to show that the role of *Phalacrocorax carbo* in the decline of the European eel is overestimated and strongly influenced by public perception (Engstrom 2001; Carpentier et al. 2009).

While the so far mentioned possible factors for the decline are more or less restricted to the continental phase of the life cycle and may vary distinctly between freshwater systems, global factors may also have to be considered when characterizing the stock decline. Several scenarios for ***climate change and associated global warming*** include the change, reduction and/or loss of the major North Atlantic current systems (Bryden et al. 2005) with an increase of average global sea surface temperature over the past 100 years being already evident (IPCC 2007). Changes in the major current systems will most likely have strong influence on the recruitment of leptocephali or glass eels to continental waters and the variability of the North Atlantic Oscillation (NAO) within the last decades might have already influenced stock densities all over Europe (Knights 2003; Bonhommeau et al. 2008a; Bonhommeau et al. 2008b; Durif et al. 2011).



Knights (2003) associated changes in the Den Oever glass eel recruitment index (DOI, Netherlands) with the North Atlantic Oscillation (NAO) and hypothesised that a change in sea surface temperature (SST) in the Sargasso Sea/Sub-Tropical Gyre (STG) has a negative impact on productivity and therefore on larval survival. Friedland et al. (2007) provided further evidence for the correlation between DOI and NOA. Even though they were not able to narrow down the list of possible reasons, they suggested changes in the ocean fronts associated with a SST warming to displace the spawning location and affect the larval transport out of the Sargasso Sea towards the continental habitats. Bonhommeau et al. (2008b) investigated whether oceanographic and trophic conditions in the Sargasso Sea influence glass eel recruitment of the European eel and could explain the recent decline. They identified two main non-exclusive processes that influence glass eel recruitment to continental waters – (1) changes in ocean current systems and associated loss in larvae numbers reaching the European continent and (2) poor food availability during the early life stages and hence low survival of leptocephali. Statistical analysis by Bonhommeau et al. (2008b) did not support a clear relationship between the position or strength of the Gulf Stream and the survival rate of larvae. Instead of the widely used NAO, their analysis focused on the Transportation Index (TI) and the Gulf Stream Index (GSI) as the NAO does not allow direct analysis of the plankton response. Thereby, it is not possible to account for possible changes in mixing and stratification and hence phytoplankton abundances associated with changes of the NOA. Nevertheless, Bonhommeau et al. (2008b) proposed a focus on the trophic conditions encountered by leptocephali in the Sargasso Sea, based on a highly significant correlation between primary production in the Sargasso Sea and recruitment numbers. Bonhommeau et al. (2008b) concluded that the shift in eel recruitment in 1982 can be associated with a change of primary production caused by SST changes in the Sargasso Sea in 1979. In an additional publication, Bonhommeau et al (2008a) were able to extend the hypothesis of a trophic linkage between global warming and the European eel recruitment onto the American and the Japanese eel populations. While most studies on oceanic influences on the European eel recruitment consider the DOI, Durif et al. (2011) tried to correlate physical and associated biological changes in the Sargasso Sea with the Skagerrak beach seine survey from Norway. This long-time fishery-independent data set on eel abundance concentrates on yellow eels living in eel grass habitats along the coast. The comparison of this marine subpopulation with the NAO again resulted in a negative correlation between sea surface temperature (SST) in the Sargasso Sea and eel abundance in the Skagerrak area (Norway) with a 12 year lag. They concluded that high SST in the Sargasso Sea might negatively influence the survival of newly hatched larvae (Durif et al. 2011). The relationship between oceanic

changes and the decline in eel recruitment has been shown by several authors. Reasons are still not entirely clear but can most likely be traced back to changes in primary production and retention of larvae in the spawning area. To eventually provide prove of responsible (non-exclusive) oceanic processes, a number of biological questions remain to be answered, e.g. food source of leptocephali and larval migrations/drift.

### **European Council Regulation No. 1100/2007**

As a result of the progressing downward trend of the European eel stock, the European Council (EC) issued Regulation No. 1100/2007 on the 18<sup>th</sup> of September 2007, to establish measures for the recovery of the European eel stock. In article 2 (§1) the regulation states that every member state of the European Union *“shall identify and define the individual river basins lying within their national territory that constitute natural habitats for the European eel”* and prepare a so-called Eel Management Plan (EMP) *“adjusted to regional and local conditions”* for each eel river basin (article 2, §3) until the end of 2008 (European Union 2007). The objective of these EMPs is to ensure a minimum of 40% spawner escapement to sea relative to the best estimate of the silver eel escapement in a pristine state without any anthropogenic activities (article 2, §4; European Union 2007). This requires a detailed description/analysis of the present situation of the eel population in each eel river basin. The regulation states (article 2, §8; European Union 2007) following measures that may be used to achieve the postulated goals:

- Reducing commercial fishing activity
- Restricting recreational fishing
- Restocking measures
- Structural measures to make rivers passable and improve river habitats, together with other environmental measures
- Transportation of silver eel form inland waters to waters from which they can escape freely to the Sargasso Sea
- Combating predators
- Temporal switching-off of hydro-electric power turbines
- Measures related to aquaculture

Member states were, however, free to decide which measures are to be enforced (European Union 2007).

Submitted EMPs were reviewed by the Commission. In case, the submitted EMP could not be approved, fishing effort had to be reduced and Member States had the chance to resubmit a revised one within three Month (article 2, §4 – 6; European Union 2007).

Even though the main focus of the Regulation 1100/2007 lies on the minimal escapement goal, it is not limited to the silver eel phase. In article 7 (§1) the regulation states that in case a Member State permits eel fisheries for eels less than 12cm, *“it shall reserve at least 60% of the eels [...] to be marketed for use in restocking [...] for the purpose of increasing the escapement level of silver eels”* (European Union 2007). The 60%, however, are set to be achieved gradually by 31 July 2013 starting with a minimum of 35% in the first year of application of an EMP (European Union 2007).

While the EMPs are limited to the designated eel river basins and thus primarily to the freshwater phase of the European eel, the regulation also broadly tries to include the Community waters seaward of the boundary of the eel river basins. Article 8 (§1) asks every Member state to either *“reduce fishing effort by at least 50% relative to the average effort deployed from 2004 to 2006”* or *“reduce fishing effort to ensure a reduction of eel catches by at least 50%”* relative to the same period (European Union 2007).

## The German Eel Management Plans

The European Commission approved all German EMPs at the 8<sup>th</sup> of April 2010 (Anonymous 2008). Out of the 10 river basins in Germany (Figure Intro-6), nine were identified to constitute eel river basins and Germany submitted individual EMPs for each of them:

- Ems
- Weser
- Eider
- Maas
- Rhein
- Schlei/Trave
- Warnow/Peene
- Elbe
- Oder

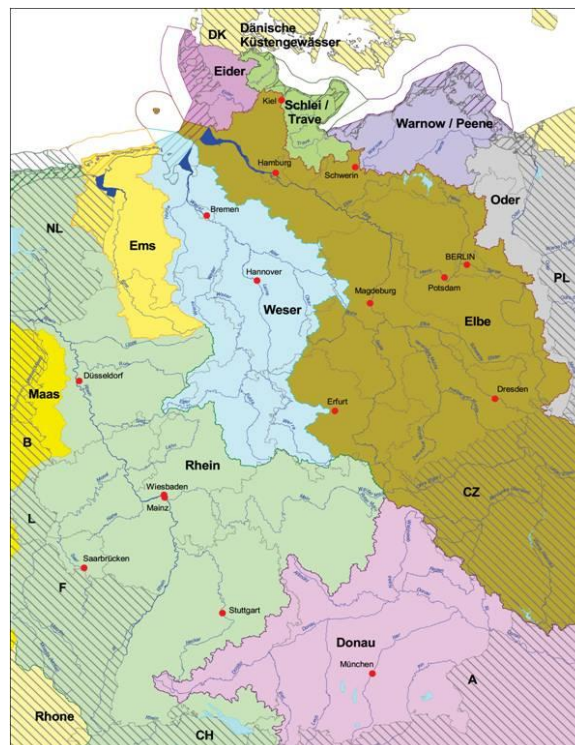


FIGURE INTRO-6 Designated (eel) river basins in Germany.  
Source: Umweltbundesamt, <http://www.umweltbundesamt.de>

The German EMPs summarize the German eel fishery which is legally regulated on federal state basis and delineate the present situation of the German eel stock (Anonymous 2008). Furthermore, the individual EMPs are giving best estimates of the 100% pristine silver eel escapement ( $B_0$ ) and respective current escapement ( $B_{current}$ ). While freshwater systems discharging into the North Sea (Ems, Weser, Elbe and Eider) are expected to support a 100% reference escapement ( $B_0$ ) of 6.9 - 9.5 kg ha<sup>-1</sup>. Inland waters flowing into the Baltic Sea (Schlei/Trave, Warnow/Peene and Oder) were rated to support distinctly lower  $B_0$  of only 1.9 – 2.8 kg ha<sup>-1</sup> (Anonymous 2008). Rhine and Maas are expected to support an intermediate pristine escapement of silver eels with 4.2 kg ha<sup>-1</sup> (Anonymous 2008). According to the German EMP, estimated  $B_{current}$  varies between 1 and 96% of the reference escapement with 4 out of the 9 eel river basins not fulfilling the goal postulated by the Regulation No. 1100/2007 (Anonymous 2008). The combined estimated  $B_{current}$ , however, constitutes about 57% of the estimated pristine escapement and thus fulfills the required 40% (Anonymous 2008). Assessing the complete current escapement of silver eels from German eel river basins is hardly possible and

numbers presented in the German EMPs are based on assumptions. For seven of the nine German EMPs a predecessor version of the German Eel Model II, the German Eel Model, was used. For the eel river basins “Eider” and “Schlei/Trave” (of which the Schwentine river system is a part of) coastal waters were included and it was thus not possible to apply the GEM (Anonymous 2008). Estimates of  $B_{\text{current}}$  had to be calculated using different approaches (Anonymous 2008):

Eel river basin “Eider”: Silver eel escapement was calculated based on “best estimates” of fisheries mortality, cormorant mortality, stock size and the assumption of several biological population characteristics. According to the EU Regulation 1100/2007, target level of escapement was determined by the use of data prior to 1980.

Eel river basin “Schlei/Trave”: Silver eel escapement was calculated based on “best estimates” of fisheries mortality, cormorant mortality, stock size and the assumption of several biological population characteristics. According to the EU Regulation 1100/2007, target level of escapement was determined by the use of data prior to 1980.

Silver eel monitoring, so far, is restricted to the German freshwater systems and hardly any information about the coastal stocks of European eels is available (Anonymous 2008). This is mainly due to the fact that, up to date, no method has been established to quantitatively assess eels in coastal waters, but will possibly cause the underestimation of the actual numbers of spawners leaving German waters.

Although most of the German eel river basins seemed to support an escapement in line with Regulation No. 1100/2007, the management authorities in Germany decided to nevertheless initiate a number of measures further strengthening the recovery of the German eel stock. Hereby, particular focus lies on the continuation/increase of stocking and the increase of the legal minimal landing size to 45/50cm (Anonymous 2008). In addition, the need for action with regard to hydropower mortality and cormorant management was highlighted (Anonymous 2008).

In 2012, the implementation of the German EMPs was reviewed (Anonymous 2012). As a result, almost all original estimates for  $B_0$  and  $B_{\text{best}}$  had to be corrected. By using the German Eel Model

II (GEM II), developed by Oeberst and Fladung (2012),  $B_0$  for Inland waters flowing into the Baltic Sea (Schlei/Trave, Warnow/Peene and Oder) was reconsidered to be  $1.5 - 3.8 \text{ kg ha}^{-1}$ , while Elbe, Eider, Maas and Rhine were estimate to support a  $B_0$  of  $0.5 - 7.2 \text{ kg ha}^{-1}$  (Anonymous 2012). Only for the eel river basins Weser and Ems, estimates for  $B_0$  were increased to 10.9 and  $16.4 \text{ kg ha}^{-1}$ . By combining all German eel river basins, the overall average  $B_0$  was therefore estimated to be approximately  $3.4 \text{ kg ha}^{-1}$  (Anonymous 2012). However, combined  $B_{\text{current}}$  from German eel river basins was estimated to represent only 38% ( $1.3 \text{ kg ha}^{-1}$ ) of  $B_0$  (instead of the originally estimated 57%) and thereby fails to fulfill the Regulation No. 1100/2007 (Anonymous 2012). However, management measures are expected to show positive feedback in the future and actual German silver eel escapement is estimated to reach the 40% milestone within 15-20 years (Anonymous 2012). New calculations of reference escapement resulted in clearly lower estimates for most eel river basins. Only Weser and Ems were reconsidered to potentially support distinctly higher escapements of  $10.9 - 16.4 \text{ kg ha}^{-1}$  (Anonymous 2012).

According to the "Draft proposal for a reporting template", the EU Regulation No. 110/2007 in addition asks for the potential current silver eel escapement without anthropogenic influences ( $B_{\text{best}}$ )(Anonymous 2012). The combined German  $B_{\text{best}}$  was estimated to be about 17% less of the current escapement, because the German European eel stock is highly influenced by pronounced stocking activities that would have to be ceased when waiving any anthropogenic influences (Anonymous 2012). Therefore, the reviewers conclude that a complete relinquishment of anthropogenic interventions (and thus ultimately also stocking) would likely lead to dramatically reduced escapement numbers (Anonymous 2012).

## AIM AND OUTLINE OF THE STUDY

Besides being a cherishable delicacy and a high-value product of freshwater fisheries all over Europe, the European eel (*Anguilla anguilla*) above all is a fascinating fish species on the edge of extinction. Scientists beyond numbers and over one hundred years of intensive research were not able to completely elicit the mysteries surrounding the European eel and it is only now that the fascinating secrets of this fish species are starting to be revealed.

The dramatic stock development of the past 30 years and the alarmingly low estimates of current recruitment and stock size document the urgent need for effective management measures all over the distribution area. The sustainable recovery of the European eel stock requires an emphatic approach in answering the remaining questions about the species' biology as numerous questions about the life of eels remain unanswered or subject of great controversy and result in management decisions based on assumptions. The European-wide distribution and the presumably panmictic population of *A.anguilla* further complicate the decision making process of management authorities. Due to the semelparous lifecycle and the relative longevity of the European eel, management measures will most likely take years (maybe even decades) to show first results (Åström and Dekker 2007) and short-term evaluation remains challenging. All the more, it is of enormous importance to carefully review the already implemented management decisions and overview possible future attempts to further impel stock recovery.

Therefore, the overall focus of the present thesis was to gain additional insights in the particular features of a local European eel stock that is facing almost all continental threats so far identified for *A.anguilla* and is at the same time subject to the implementation of already established recovery measures. The results given here are of particular interest, because the investigated local eel stock entirely depends on stocking and should therefore be considered to be artificially maintained. All chapters relate to the silver eel output of a small-scale freshwater system in northern Germany. Due to the particular features of the investigated freshwater system, this thesis documents the rare possibility to directly assess the actual silver eel escapement. Thereby, it was possible to evaluate current management measures on a local scale and identify short-comings in the attempt to impel the European eel stock recovery. It was investigated, what factors influence the silver eel output of a small-scale freshwater system and to what extend such a system is yielding silver eels that potentially contribute to stock recovery (**Chapter I**). So far, implementing the EU Regulation No. 1100/2007 had to be based on a number of assumptions often based on model outputs. Up to date, however, it was hardly possible to to

evaluate how close to reality these assumptions are. This is mostly due to the fact that the direct assessment of escapement numbers is hardly possible for the entire eel river basins. The present thesis and the it's restriction on a small-scale freshwater system, for the first time, compares actually documented silver eel escapement with the estimations given by the German Eel Model II and thereby allows for evaluating the effectiveness of current management measures (**Chapter II**). Furthermore, the thesis documents the necessity to extend current management of *A. anguilla* to the continental coastal waters in order to ensure the highest possible spawner escapement (**Chapter III**).

**Chapter I (“Silver eel escapement and quality in an exemplary German river system”)** summarizes the work of a 3-year silver eel monitoring program in the Schwentine River system close to Kiel. It documents the environmental conditions and local anthropogenic influences that affect the overall number of emigrating silver eels and the timing of escapement as well as the quality of silver eels that are eventually leaving the system to migrate to the spawning. The results help to understand peculiarities of the local silver eel escapement and highlight the necessity to consider local environmental and biological features to ensure the highest possible effectiveness of management measures.

As the number of escaping silver eels is one of the few parameters that at least partly allows the evaluation of management measures in the short-term, chapter II (**“Model Prediction vs. Reality – Testing the predictions of a European eel (*Anguilla anguilla*) stock dynamics model against the in situ observation of silver eel escapement in compliance with the European Eel Regulation”**) compares the documented escapement from the Schwentine River system with the output of the German Eel Model (GEM II) that was used in the German Eel Management Plan (EMP). Thereby, it was possible to revise the potential of the model and highlight the importance of high-quality datasets to ensure a sound basis for management decisions.

Unfortunately, up to date management of the European eel primarily focuses on the continental phase. Most of the time, escapement goals are restricted to freshwater systems and migratory success has not been in the focus of management authorities so far. However, to impel the stock recovery not only the number of silver eels leaving freshwater is of implicit importance, but also the migratory and reproductive success will inevitably affect the future recruitment and stock size. Therefore, in **chapter III (“Tracking the migration success of stocked European eels (*Anguilla anguilla*) in the Baltic Sea”)** it was investigated, whether eels that had experienced



considerable translocations prior to stocking and were thus not able to imprint migration routes back to the spawning ground eventually are capable of target-oriented migratory behavior or are rather lost in migration and therefore from the effective population size. Thereby, the necessity to extend the management of the species onto a larger geographical level was highlighted.

# CHAPTER I - A long way down – Escapement success of silver eels from a German river system

L. Marohn<sup>1,2</sup>, E. Prigge<sup>1</sup>, R. Hanel<sup>1,2</sup>

<sup>1</sup>Helmholtz Centre for Ocean Research (GEOMAR), Duesternbrooker Weg 20, 24105 Kiel, Germany

<sup>2</sup>vTI - Institute for Fisheries Ecology, Palmaille 9, 22767 Hamburg, Germany

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## ABSTRACT

1. The European eel (*Anguilla anguilla*) stock had experienced a sharp decline during the last decades and is suffering from massive anthropogenic impacts on inland waters. To evaluate the benefit of different management measures and to better understand the contribution of individual drainage systems to eel spawner production, direct escapement assessments are required. Moreover, the role of environmental triggers for the onset of silver eel escapement requires better understanding to reduce the impact of fisheries and turbine mortality on migrating eels.

2. In this study total female silver eel escapement from a northern German drainage system was assessed over a period of three consecutive years. At the same time river discharge and water temperatures were examined. Commercial and recreational fisheries landing data were compared to records of restocking effort to estimate the benefit of restocking for spawner production and fisheries. Lipid content and infestation with the swim bladder parasite *Anguillicoloides crassus* were assessed as fitness parameters and trash rack mortality at the hydropower station was determined.

3. Results reveal that the number of eels leaving the Schwentine River is far below expected values for the corresponding river basin district, pointing out the importance of the use of high quality river-specific data when modeling silver eel escapement. High migration activities during short time periods in autumn in connection with environmental triggers suggest that a precise prediction of escapement events is possible. However, high fishing and trash rack mortalities as well as high *A. crassus* intensities of infection are matters of concern.

## INTRODUCTION

During the 20th century the human impact on European river systems increased rigorously and reached an almost ubiquitous level. Diadromous species including the European eel (*Anguilla Anguilla*, Linnaeus 1758) are specifically affected by the severe modification and deterioration of habitats. The strong decline of eel recruitment since the 1980s and the currently observed low stock size (ICES, 2011a) are considered to be caused by a combination of reduced habitat quality including river discontinuity, high fishing mortalities and possible climatic changes (Knights, 2003; ICES, 2006; Belpaire et al., 2009). The European commission recognized the increase of silver eel escapement from freshwaters as essential for stock recovery and changed its legislation accordingly (EU, 2007). European member states must now implement management measures to guarantee the escapement of silver eels from river basins to 40 % of the best estimated number of eels that would have escaped under pristine conditions (EU, 2007). Not to mention the difficulties when estimating the pristine size of a stock, even the accurate quantification of present silver eel escapement is methodologically challenging. However, a reliable assessment of silver eel escapement is required to evaluate the benefit of the implemented measures. As a consequence, escapement is often estimated indirectly either by mark-recapture studies or modeling approaches (Feunteun, 2000; Arahamian et al., 2007; Breukeaar et al., 2009; Verbiest et al., 2012), whereas direct censuses are scarce. A direct assessment of escapement is further complicated by the lack of reliable information on environmental triggers for the onset of spawning migration and missing knowledge on the time and duration of major escapement events. Such knowledge could improve the predictability of escapement events and therefore help to trigger temporal turbine shutoffs and closed seasons for fisheries. Previous studies indicated that main downstream eel migration takes place during autumn and is predominantly nocturnal (Vøllestad et al., 1986; Breukeaar et al., 2009; Aarestrup et al., 2010; Davidsen et al., 2011; Palstra et al., 2011). Among others, river discharge, water temperature and lunar phase were shown to affect silver eel escapement (Tesch, 1999; Haraldstad, Vøllestad & Jonsson, 1985; Vøllestad et al., 1986; Feunteun et al., 2000; Travade et al., 2010). However, results are often controversial and seem to depend on regional fluvial characteristics.

Whether and to what extent a specific river basin may contribute to the effective spawning biomass of the European eel is not only the result of the number of escaping eels but also a matter of spawner quality. Introduced parasites and reduced energy reserves are suspected to be a significant threat for European eels as they may impair long term swimming ability and

therefore reduce the probability for spawners to reach their spawning grounds in the Sargasso Sea (Sprengel & Lüchtenberg, 1991; Palstra et al., 2007; Clevestam et al., 2011).

Among measures that locally increase silver eel escapement, restocking of young eels into freshwaters is a viable but highly controversially debated option. Several European countries try to comply with European Union regulations through translocation of juvenile eels from estuarine to inland waters. But if these glass eel stocking programs really have a net benefit for the overall stock has never been scientifically proven. In its last advice, the International Council of the Exploration of the Sea (ICES, 2011a) reiterates its concern that restocking programs are unlikely to contribute to the recovery of the European eel stock and stresses the need for a risk assessment prior to any stocking activity, taking into account fishing, holding, transport, post-stocking mortalities and other factors such as disease and parasite transfers.

The aim of this study was to assess total silver eel escapement from a northern German river system (Schwentine River) as an output control and to evaluate the reliability of escapement estimations used in the German Eel Management Plan (EMP). Furthermore, escapement numbers together with commercial and recreational fisheries landing data were compared to records of restocking effort to estimate the benefit of restocking for spawner production and fisheries in an enclosed system. In addition, potential migration peaks and triggers for the onset of spawning migration should be identified. For that reason the overall escapement of female silver eels was assessed during three consecutive years. The setup enabled the catch of almost all downstream migrating female silver eels at a fish ladder bypassing a hydropower station. Moreover, the muscle fat content and *Anguillicoloides crassus* (*Anguillicoloides crassus*, Kuwahara, Niimi & Itagaki 1974) infestation of escaping silver eels were assessed as fitness proxies and trash rack mortality at the hydropower station was determined. This study provides empirical data about patterns of downstream silver eel migration and delivers information on silver eel quality and survival in an enclosed Baltic Sea tributary system. The benefit of restocking is discussed regarding its contribution to either fisheries or silver eel escapement.

## **MATERIAL AND METHODS**

### **STUDY AREA**

The Schwentine River has a length of 62 km and drains into the western Baltic at the city of Kiel (Figure I-1). The river system consists of two major river arms and a lake district and has a water surface of approximately 7500 ha. It is fished by six commercial fishers and provides a popular area for recreational fisheries with approximately 1500 resident sport fishers that are organized in sport fishing associations and an unknown number of unorganized anglers that occasionally

fish. Since the beginning of the 20th century the river is blocked in the lower reaches by three barriers, including two closely spaced hydropower stations that block any upstream and largely impede downstream migration of fish.

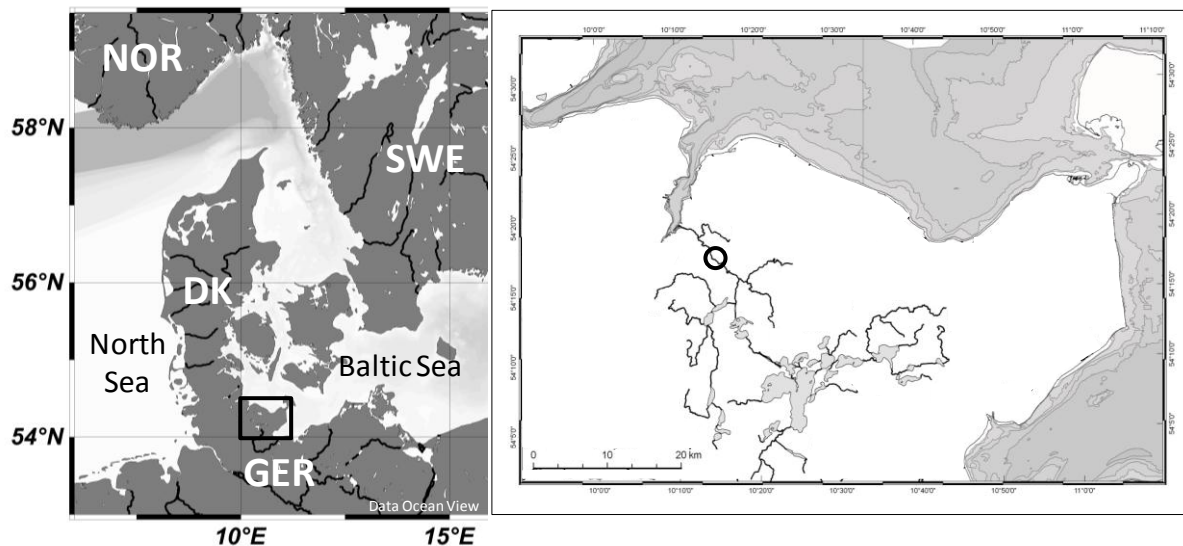


FIGURE I-1 Sampling area. The sampling station is indicated by the black circle.

#### SILVER EEL ESCAPEMENT

Throughout three consecutive years, eels were sampled at the uppermost hydropower station. It is located approximately 9 km upstream from the river mouth and provides the first barrier for downstream migrating eels (Fig. 1). Two bypasses allow fish to migrate downstream. One surface bypass that flows into a helix fish pass and a deep bypass, with a 300 mm diameter that starts at bottom level adjacent to the trash rack that is mounted in front of the turbines. The trash rack has a light spacing of 20 mm and is equipped with an automatic debris cleaner. In order to catch all fish moving through the bypasses both were completely blocked with traps. In addition, the debris container attached to the trash rack cleaning device was regularly screened for perished eels. Every caught eel was weighed and photographed for subsequent length measurements. Total length of every individual eel was measured using Image Tool 3.0 (developed by the University of Texas Health Science Center, San Antonio; UTHACSA) calibrated according to a scale depicted in the photo. Chang, Di Nardo & Lin (2010) used a similar procedure to measure Albacore tuna (*Thunnus alalunga*) with an accuracy of approximately 2.1%. Eels were assigned to one of the six maturity stages according to the classification defined by Durif, Dufour & Elie (2005). If eels were frozen prior to measurements, lengths and weights were corrected for reduction according to Wickström (1986). Only eels that were assigned to the

stages SFIV and SFV were considered to be real migrating female silver eels and included in the escapement census. A total number of 228 silver eels were sacrificed for further analyses.

In cases of extreme water levels a flap gate at the hydropower station automatically opened and water was spilled from the reservoir. Moreover, Adam et al. (1998) and Calles et al. (2010) documented the general ability of eels up to 70 cm length to pass trash racks with spacings of 20 mm under laboratory conditions. To estimate size and number of eels that were able to pass through the opened flap gate or the trash rack and to correct the escapement numbers accordingly, 36 migrating female silver eels were tagged with implanted active transponders (Acoustic Transmitter Tags (V9; VEMCO, Canada)) and released upstream the hydropower station. A combination of three VR2W monitoring receiver (VEMCO, Canada) was installed to ensure the detection of all eels that passed through the hydropower station without being caught and counted. Two receivers were placed in the reservoir upstream and one approximately 200 m downstream the hydropower station. They were active for 271 days and minimum battery life of the transmitters was estimated to be 153 days by the manufacturer. Eels were released between September 2011 and January 2012. Their length varied from 70.6 cm to 97.5 cm and their weight from 586 g to 1595 g. Since males are usually expected to not exceed a total length of around 35 to 46 cm (Tesch 1999), they are assumed to be underrepresented in the samples and were thus not included in the analysis at all.

During the entire sampling period surface water temperatures were measured by a TidbiT v2 data logger (Onset; Bourne, USA) at the hydropower station. River discharge was assessed at a discharge site approximately 9 km upstream the hydropower station.

#### CATCH AND RESTOCKING DATA

Landing statistics of commercial eel fisheries for the years 2000 to 2010 and historical restocking data for the years 1993-2010 were provided by the State Agency for Agriculture, Environment and Rural Areas (LLUR) of the German region of Schleswig-Holstein. Data gaps in landing statistics were filled with annual mean catches per ha of the entire river system in respective years. In order to estimate the length distribution of eels in commercial catches, subsamples of landings of two fishers were measured (N = 218). Catches of the recreational fishery were assessed by collecting catch data of two representative sport fishing associations for the years 2000 to 2009. An average annual eel catch per angler was determined which allowed an estimation of the overall annual eel catch of all organized sport fishers in the Schwentine river system. The catch of anglers that were not organized in sport fishing clubs was not assessed.

### SILVER EEL QUALITY

Total lipid content of 93 silver eels was determined. Approximately 50 g of bone free white muscle tissue and skin from a cross section in front of the anus was homogenized. Fat was chemically extracted from a subsample of 5 g of the homogenate by using a isopropanol:cyclohexan (16:20) solution (Carl Roth; Karlsruhe, Germany). By adding water, lipids were transferred into the cyclohexan phase. Phases were separated by centrifugation. Lipid content was determined gravimetrically and expressed as per cent of tissue weight. A detailed description of the method is given in Karl et al. (2012).

To investigate the impact of potentially harmful parasites on silver eels from the Schwentine River, prevalence and intensity of infection with the swim bladder nematode *Anguillicoides crassus* was determined. Swim bladders of 118 silver eels were macroscopically analyzed and *A. crassus* individuals were counted. In addition, the swim bladder damage of 79 silver eels was assessed, following the classification key of Hartmann (1993), which ranges from no visible damage (class 1) to heavily thickened walls, reduced lumina and no gas content (class 5).

### AGE DETERMINATION

The age of 87 downstream migrating silver eels was determined by otolith reading. Otoliths were dried at air for at least 48 hours. Subsequently, they were cut transversally through the core and burned in a Bunsen burner for approximately 30 seconds. Annuli were counted according to the manual published by the "ICES Workshop on Age Reading of European and American Eel" (ICES 2011b). For quality control each otolith was read by two persons and was refused when no agreement was reached.

### SPECIES IDENTIFICATION

The uncontrolled global trade with eels for hatcheries and restocking purposes caused the introduction of a considerable amount of American eels (*Anguilla rostrata*, Le Sueur 1817) into European waters (Frankowski et al., 2009). In order to assess the amount of *A. rostrata* in the Schwentine River and estimate its potential influence on the results of this study, genetic species identification was conducted on mitochondrial cytochrome b and 18S rDNA gene fragments of 142 silver eels. The method of Frankowski & Bastrop (2010) was modified as described in Prigge, Marohn & Hanel (in prep.).

## STATISTICAL ANALYSIS

Statistica 8.0 (StatSoft Inc.; Tulsa, USA) and the R statistical language (version 2.15.1) were used for statistical analysis. Cumulative numbers of escaping silver eels per calendar week were used for statistical analyses. Regression analysis was performed to test for correlations between silver eel escapement and date, water discharge and water temperature. Analysis of Variances (ANOVA) or Kruskal-Wallis Test was used to test for differences in escapement between four moon phases and for yearly differences in water temperature (daily mean) and in river discharge (daily mean). Furthermore, Kruskal-Wallis Test tested for differences in summer (Jul-Aug) and August temperatures as well as in early autumn river discharge (Aug-Oct) between years. The influence of age on *A. crassus* intensity of infection was analyzed by a regression analysis. A significance level of  $p = 0.05$  was applied to all tests.

## RESULTS

### SILVER EEL ESCAPEMENT

During the entire 3 years sampling period 1,285 eels were counted. 935 of those were migrating female silver eels (maturity stages SFIV and SFV) with a total weight of 992 kg. The rest almost entirely consisted of eels of maturity stages SFII (growth phase) and SFIII (pre-migrant phase) and was not included into escapement numbers. Only three males were caught. Numbers of escaping female silver eels varied between years, but their fraction from total catch was constantly between 72.5% and 73.1%. In 2009, 97 silver eels (105 kg) were caught, 512 (530 kg) in 2010 and 319 (358 kg) in 2011. The age of escaping silver eels ranged from 5 to 28 years. However, these extreme values were only detected sporadically. 90% of all migrating female silver eels left the system at ages between 9 and 23 years and 75% between 10 and 20 years.

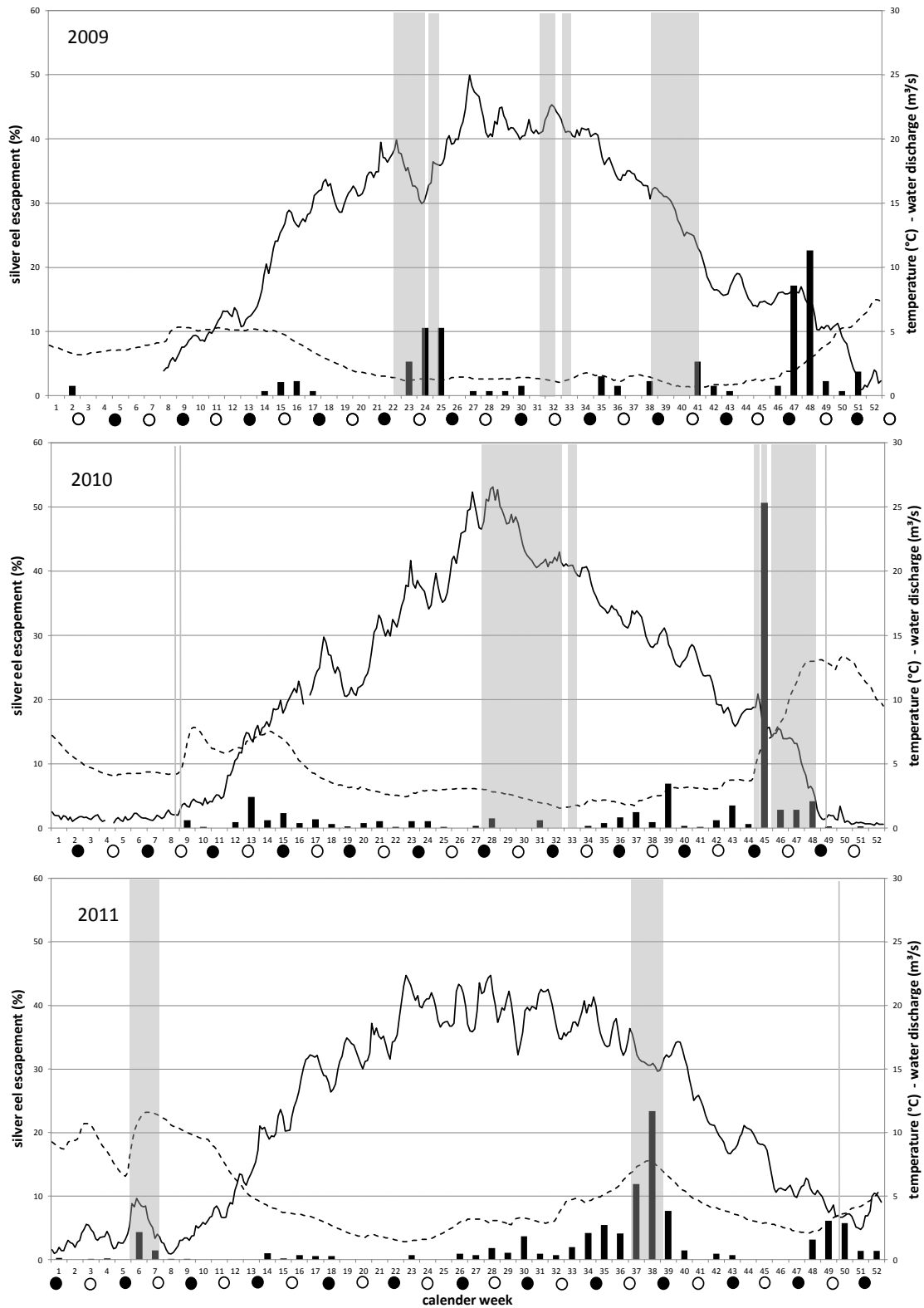
At times of free river discharge caused by open flap gates it was not possible to record all escaping silver eels. Such events lasted 50 days in 2009, 61 days in 2010 and 27 days in 2011 (Figure I-2). During November 2010 and September 2011 spillage took place during periods of increased silver eel migration. The additional number of silver eels that potentially escaped during these periods was estimated by using mark recapture data. During a 26 day period of uncontrolled water release in January 2012 seven out of 36 tagged silver eels that were released upstream the hydropower station passed the hydropower station through the open flap gate. In the same period one tagged specimen was caught in a trap while migrating downstream. For further analyses, all catch data during periods of spillage were corrected accordingly (factor 7). This resulted in an annual silver eel escapement of 133 specimens in 2009 (144 kg;  $0.02 \text{ kg ha}^{-1} \text{ y}^{-1}$ ), 683 in 2010 (691 kg;  $0.09 \text{ kg ha}^{-1} \text{ y}^{-1}$ ) and 544 in 2011 (577 kg;  $0.08 \text{ kg ha}^{-1} \text{ y}^{-1}$ ).



Regression analysis revealed a seasonal influence (calendar week) on silver eel escapement ( $p = 0.0096$ ) with an increase in the number of escaping eels over the year (Figure I-2). The average escapement accounted for 5.1% (SD  $\pm 3.1$ ) and 15.8% (SD  $\pm 14.6$ ) of the total annual escapement for the first and second quarters of the year, respectively. Main migration events occurred in the second half of the year. On average 31.4% (SD  $\pm 31.6$ ) and 47.7% (SD  $\pm 23.9$ ) of the silver eel migrants were recorded in the third and fourth quarter, respectively. However, higher escapement numbers later in the year were not caused by permanently increasing migration activities but by single migration events. In 2009 39.8% of all escaping silver eels migrated during two weeks at the end of November and 50.6% of the annual silver eel run in 2010 migrated during one week in mid November. In 2011 migration peaks were less distinct. 56.8% escaped during six weeks from end of August until the end of September, while the escapement peak during November and early December accounted for 35.0% of annual escapement (Figure I-2).

Regarding potential triggers of migration, river discharge was the only factor that had a significant effect on silver eel escapement. A positive correlation between river discharge and escapement was observed ( $p = 0.0468$ ). No significant correlation of escapement and water temperature ( $p = 0.8515$ ) was detected nor seems moon phase to influence the time of migration ( $p = 0.9132$ ).

Annual river discharge significantly differed between years. It was lower in 2009 compared to 2010 and 2011 ( $H(2, 156) = 25.99$ ;  $p = 0.000$ ) (Figure I-2). During early autumn (Aug - Oct) it was significantly increased in 2011 compared to 2009 and 2010 ( $H(2, 276) = 230.5$ ;  $p = 0.000$ ). Values averaged  $1.2 \text{ m}^3 \text{ s}^{-1}$  (SD  $\pm 0.3$ ),  $2.5 \text{ m}^3 \text{ s}^{-1}$  (SD  $\pm 0.7$ ) and  $5.1 \text{ m}^3 \text{ s}^{-1}$  (SD  $\pm 1.4$ ) from 2009 to 2011, respectively. Temperature records started at February 20th 2009. Therefore, only mean annual temperatures between February 20th and December 31st were compared between years. ANOVA detected no significant differences ( $F(2, 851) = 1.216$ ,  $p = 0.2969$ ) (Figure I-2). However, summer temperatures (Jul – Aug) and August temperatures changed significantly among years. Summer temperatures averaged  $21.2^\circ\text{C}$  (SD  $\pm 1.2$ ),  $21.8^\circ\text{C}$  (SD  $\pm 2.6$ ) and  $19.3^\circ\text{C}$  (SD  $\pm 1.4$ ) from 2009 to 2011, respectively ( $H(2, 8928) = 2280.4$ ;  $p = 0.000$ ). Mean August temperatures were  $20.8^\circ\text{C}$  (SD  $\pm 1.0$ ),  $19.8^\circ\text{C}$  (SD  $\pm 1.3$ ) and  $19.2^\circ\text{C}$  (SD  $\pm 1.3$ ) from 2009 to 2011, respectively ( $H(2, 4464) = 926.4$ ;  $p = 0.000$ ).



**FIGURE I-2** Corrected silver eel escapement during the years 2009-2011. Black bars represent per cent of the annual silver eel escapement. Solid lines depict water temperature and dashed lines river discharge. Grey areas represent time periods of spillage. Moon phase is indicated by symbols (● = new moon and ○ = full moon).

## CATCH AND RESTOCKING DATA

During 2000 and 2010 annual eel catches of commercial fishermen averaged  $7,808 \text{ kg y}^{-1}$  ( $\text{SD} \pm 1,207$ ), which corresponds to  $1.04 \text{ kg ha}^{-1}\text{y}^{-1}$ . State Agency landing statistics for all inland waters in the river basin district documented an average silver eel proportion in the commercial catches of 34.2% (LLUR, 2008). Accordingly, annual average silver eel landings in the Schwentine River from 2000 to 2010 accounted for  $0.36 \text{ kg ha}^{-1}\text{y}^{-1}$ . During the years 2009 and 2010, silver eel catches in the Schwentine River were below the ten-year average.  $0.24 \text{ kg ha}^{-1}\text{y}^{-1}$  and  $0.30 \text{ kg ha}^{-1}\text{y}^{-1}$  silver eels were caught in 2009 and 2010, respectively. Length distribution in catches is given in Figure I-3.

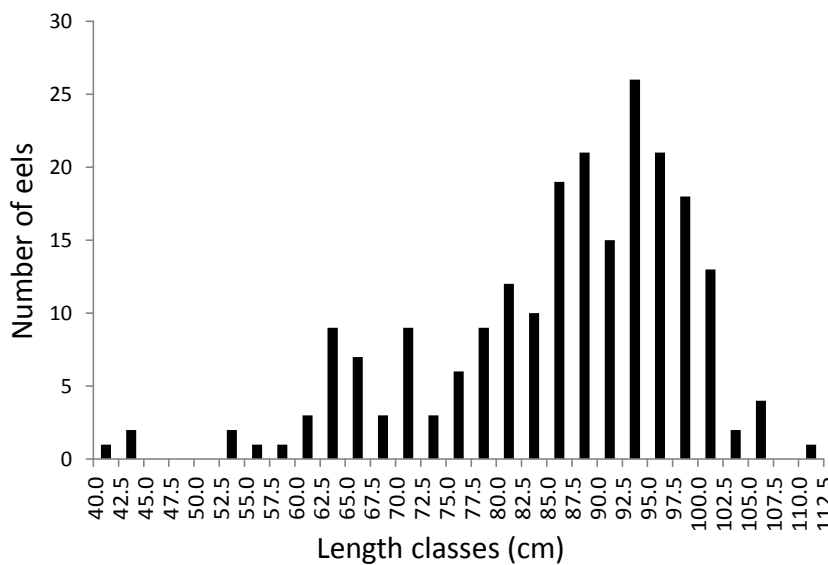


FIGURE I-3 Length-frequency of eels in commercial catches

The estimated average of annual recreational eel catches during the years 2000 to 2009 was  $1,340 \text{ kg y}^{-1}$  ( $\text{SD} \pm 752$ ) corresponding to  $0.9 \text{ kg angler}^{-1}\text{y}^{-1}$  and  $0.18 \text{ kg ha}^{-1}\text{y}^{-1}$ . Due to the lack of reliable information on a differentiation between yellow and silver eels caught by recreational fishers these catch data include eels of all development stages. Applying silver eel proportions from commercial catches, annual recreational silver eel catches account for  $0.06 \text{ kg ha}^{-1}\text{y}^{-1}$ . In 2009 recreational eel fishers landed only around 830 kg corresponding to  $0.04 \text{ kg silver eel ha}^{-1}\text{y}^{-1}$ .

The average annual amount of restocked eels between 1993 and 2010 was  $2,795 \text{ kg}$  ( $\text{SD} \pm 944$ ) ( $0.4 \text{ kg ha}^{-1}\text{y}^{-1}$ ). Before 2005 all years but one exceeded the average, whereas after 2005 all values were below, indicating a decreasing trend in restocking activities. Values decreased from

around 3,500 kg y<sup>-1</sup> during the 1990s to around 1,200 kg between 2007 and 2009. In 2010 restocking activities increased again and reached 2,300 kg.

#### TRASHRACK MORTALITY

32.2% of all migrating silver eels were impinged in the trash racks and died either through the compacting pressure or after being captured by the automatic debris cleaner (Table I-1). During most escapement events trash rack mortality remained below 0.2% of total escapement. Only during two silver eel runs in late autumn of the years 2010 and 2011 it reached high levels. In November 2010 77% of all eels caught at the hydropower station were impinged in the trash rack. In December 2011 the fraction of killed eels reached 70% during a minor escapement event, whereas the earlier migration peak during September 2011 resulted in almost no eel mortality at the trash rack. The flap gate was closed during high trash rack mortalities. Length distribution of eels impinged in the trash rack did not differ from the distribution of individuals caught in the fish pass, but the minimum length of eels caught in the fish pass was considerably smaller (Table I-1).

**Table I-1 Length distribution of eels caught in bypasses and being impinged in the trash rack**

	N	%	min length (cm)	max length (cm)	10 <sup>th</sup> percentile (cm)	25 <sup>th</sup> percentile (cm)	75 <sup>th</sup> percentile (cm)	90 <sup>th</sup> percentile (cm)
Bypass	871	67.8	31.5	112.4	< 66.6	< 73.6	< 88.3	< 95.4
Trash rack	414	32.2	54.4	104.4	< 67.0	< 72.0	< 89.0	< 96.0

#### ACOUSTIC TELEMETRY

From 36 silver eels tagged with acoustic transmitters, eight specimens were recaptured at the hydropower station. Another four have passed the hydropower station and have been detected at the downstream receiver station. These eels escaped during spillage through the open flap gate. During the same time period contact was lost to another three eels. The majority of tagged eels interrupted their migration after release. Twelve individuals migrated back upstream and another seven specimens remained in the first 500 m above the hydropower station for the rest of the battery life. The fate of two specimens remained unclear. Details and results of the telemetry study are summarized in Table I-2.

Table I-2 Size, detection period and fate of tagged eels

Eel #	length (cm)	weight (g)	release date	last detection	last location
1	79.8	1070.0	23.09.2011	27.09.2011	recaptured
2	82.4	940.5	01.12.2011	07.12.2011	recaptured
3	77.5	884.0	01.12.2011	05.12.2012	recaptured
4	85.9	1096.0	07.12.2011	10.12.2011	recaptured
5	79.5	1025.2	08.12.2011	02.01.2012	recaptured
6	72.9	716.2	08.12.2011	12.12.2011	recaptured
7	96.0	1686.7	06.01.2012	10.02.2012	recaptured
8	87.6	1232.9	06.01.2012	24.01.2012	recaptured
9	82.7	967.7	09.09.2011	04.01.2012	escaped
10	78.8	672.6	07.12.2011	06.01.2012	escaped
11	91.3	1368.0	06.01.2012	20.01.2012	escaped
12	80.0	810.5	06.01.2012	07.01.2012	escaped
13	72.4	713.7	01.12.2011	13.01.2012	most likely escaped
14	85.2	1301.7	01.12.2011	04.01.2012	most likely escaped
15	79.8	955.4	08.12.2011	05.01.2012	most likely escaped
16	73.5	726.7	30.09.2011	07.03.2012	remained upstream
17	97.5	1595.0	07.10.2011	27.03.2012	remained upstream
18	79.6	965.5	21.10.2011	27.03.2012	remained upstream
19	70.6	585.9	26.10.2011	01.04.2012	remained upstream
20	77.2	921.7	02.11.2011	09.04.2012	remained upstream
21	77.9	1015.6	01.12.2011	01.05.2012	remained upstream
22	78.0	1011.9	07.12.2011	14.05.2012	remained upstream
23	76.2	776.2	07.09.2011	01.10.2011	migrated upstream
24	74.3	835.0	23.09.2011	03.01.2012	migrated upstream
25	91.5	1455.0	23.09.2011	23.09.2011	migrated upstream
26	79.4	945.0	23.09.2011	23.09.2011	migrated upstream
27	86.8	1253.3	30.09.2011	01.10.2011	migrated upstream
28	81.4	1091.2	07.10.2011	11.10.2011	migrated upstream
29	83.6	978.4	21.10.2011	25.03.2012	migrated upstream
30	76.5	729.6	26.10.2011	26.10.2011	migrated upstream
31	77.4	726.0	04.12.2011	28.12.2011	migrated upstream
32	80.0	918.8	08.12.2011	22.04.2012	migrated upstream
33	76.0	854.0	04.01.2012	02.05.2012	migrated upstream
34	87.7	1138.6	06.01.2012	18.05.2012	migrated upstream
35	72.0	1405.0	30.09.2011	04.10.2011	unknown fate
36	70.6	714.1	08.12.2011	05.03.2012	unknown fate

## SILVER EEL QUALITY

The assessment of silver eel quality included the determination of energy resources (fat content) and infestation with the swim bladder parasite *A. crassus*. Mean fat content of 79 analyzed silver eels was 27.3% (SD  $\pm$  3.0). It ranged from 21.6% to 36.1%. Fifty eels (64.9%) had fat contents between 25% and 30% and 11 eels (14.3%) exceeded fat levels of 30%. Prevalence of *A. crassus* in escaping silver eels was high. In 79.9% of all analyzed swim bladders (N = 118) the nematode was detected. 21.4% had infection intensities above ten parasites and were considered to be severely infected. Most analyzed specimens showed visible but moderate swim bladder damages (Hartmann class 2 and 3; 89.2%), whereas 4.3% were classified as severely damaged (Hartmann class 4) (Hartmann, 1993). Only 6.5% were unaffected (Hartmann class 1). 73.3% of

all nematode free swim bladders showed signs of earlier infections. Intensities of *A. crassus* infections were not dependent on age of the hosts (regression analysis  $p = 0.5841$ ).

#### SPECIES IDENTIFICATION

Of 142 analyzed silver eels seven individuals were identified as *A. rostrata* (4.9%). Projected to the annual silver eel escapement from the Schwentine River this corresponds to a number of 7, 33 and 27 *A. rostrata* in 2009, 2010 and 2011, respectively. This number is assumed to be too low to bias the results presented here.

### DISCUSSION

#### SILVER EEL ESCAPEMENT

Observed annual silver eel escapement from the Schwentine River was low. The EMP estimated the current silver eel escapement of the respective river basin district (Schlei/Trave) to account for 33% of the expected escapement under pristine conditions (Anonymus, 2008). This would correspond to an escapement of  $0.49 - 1.24 \text{ kg ha}^{-1}\text{y}^{-1}$  and is far above the here monitored values ( $0.02 - 0.09 \text{ kg ha}^{-1}\text{y}^{-1}$ ). This result points out that the accuracy of indirect estimations of silver eel escapement from rivers is a matter of concern and should be used with caution. The EMP estimated current silver eel abundance and silver eel escapement from the Schlei/Trave river basin on the basis of commercial landing data and estimated mortality factors (fishery, cormorant, turbines). To generate a realistic estimation of silver eel escapement from inland waters a careful and river specific assessment of these parameters is required. As shown by Prigge et al. (in prep.) a good agreement between modeled and monitored escapement numbers can only be achieved by the labor intense assessment of river specific mortality factors and the use of adequate models (Prigge et al., in prep.). In contrast, the use of low quality data entails the risk of substantially overestimating silver eel escapement, which severely counteracts efforts for the restoration of the European eel stock.

Effort is also needed to improve the predictability of escapement events. The here presented results are in accordance with a number of studies that indicate that monitoring of only a few environmental parameters could help to predict the main downstream migration events of silver eels. Highest migration activity in the Schwentine River was observed between August and December which corresponds to the general observation of main silver eel escapement in autumn (Tesch, 1999; Vøllestad et al., 1986; Haro, 2003). However, time, intensities and patterns of escapement events clearly differ among years. While distinct migration events were observed in November 2009 and 2010, main escapement in 2011 extended over five weeks in

August and September. These results match with escapement patterns described by Durif & Elie (2008a), who suggested that average August temperatures might influence the onset of spawning migration, with lower temperatures resulting in an earlier start of migration. The here presented results support this hypothesis. Although temperature differences between years were rather small, the combination of lower temperatures and elevated discharge levels in 2011 might have caused an earlier onset of migration. This supports findings of Vøllestad et al. (1986), who explained yearly differences in the onset of downstream migration with differences in summer temperatures and river discharge. However, clear temperature thresholds for the initiation of migration events seem not to exist. In this study almost 90% of all escaping eels migrated at water temperatures between 6°C and 18°C but a specific temperature at the onset of downstream migration was not observed. This is consistent with previous studies that observed downstream migration of silver eels during a wide range of water temperatures (Haraldstad et al., 1985; Vøllestad et al., 1986). In this study highest escapement activity was detected at 8°C confirming results of Vøllestad et al. (1986). Although a direct relationship of water temperature and silver eel escapement was not detectable, these findings suggest that temperature is among the factors influencing eel migration. A more important factor influencing timing and intensity of silver eel escapement is river discharge. In the Schwentine River every observed escapement event during the three year monitoring period was accompanied by an increase in river discharge. Although high river discharges did not always cause an increase of escapement rates and in other rivers highest escapement rates were observed at medium water discharges (Haraldstad et al., 1985), the clear positive influence of water discharge on migration activity indicates its feasibility for the prediction of escapement events. In contrast, no influence of moon phase on migration activity was observed. Although light conditions might be of interest when predicting eel downstream migration (Tesch, 1999; Haro, 2003; Davidsen et al., 2011), lunar periodicity alone seems to be of minor importance and provides an unfeasible indicator for migration activity. The here presented results indicate that a careful observation of river discharge and water temperatures between July and December could suffice to determine potential periods of high downstream migration activity of silver eels.

Although eel escapement assessment in the present study was monitored directly and is not based on assumptions it must be considered that the results are biased to a certain degree. The number of escaping female silver eels below 70 cm was presumably underestimated since these individuals could have escaped through the 20 mm trash rack in front of the turbines (Adam et al., 1998; Calles et al., 2010). However, this error is assumed to only moderately affect the here presented escapement numbers. Catch data from the German Data Collection Framework for

eels indicate that in German waters only 23.4% of female eels below a total body length of 70 cm are migrating silver eels (Thünen-Institute of Fisheries Ecology, unpublished data) and representative landing data from the Schwentine River showed that only 13.3% of silver eels are below 70 cm. The proportion of small female silver eels from total escapement can therefore be assumed to be small and a quantitative assessment of small female silver eels would not have increased escapement numbers considerably.

In any case, trash rack spacings were too wide for a quantitative determination of male silver eels, which only reach maximum sizes of about 46 cm (Tesch, 1999). However, only 25% of all sampled eels with body sizes below 47 cm were male silver eels, indicating that the Schwentine River represents a female dominated river system. This assumption is supported by the observation, that temperate latitudes support the development of female eels (Wickström, Westin & Clevestam, 1996; ICES, 2010). It can therefore also be assumed that the detection of escaping males would not have significantly increased total silver eel escapement numbers.

#### SILVER EEL FISHERIES AND OTHER REASONS FOR ESCAPEMENT FAILURE

Silver eel fisheries landings in the Schwentine River exceeded silver eel escapement by far and appear to be a major reason for the low silver eel output. Commercial average annual silver eel catches accounted for  $0.36 \text{ kg ha}^{-1}\text{y}^{-1}$  and total annual average eel landings reached  $1.04 \text{ kg ha}^{-1}\text{y}^{-1}$ . Current fishing pressure in the Schwentine River is high and consequently the average annual restocking of almost 3,000 kg of juvenile eels is basically enabling and supporting eel fisheries and only to a much lesser extent contributes to stock recovery. Average annual recreational catches seem to be underestimated in the current study. Between 2000 and 2009 they accounted for  $0.18 \text{ kg ha}^{-1}\text{y}^{-1}$ . Applying silver eel proportions from commercial catches, annual recreational silver eel catches amount for  $0.06 \text{ kg ha}^{-1}\text{y}^{-1}$ . Estimations from the State Agency resulted in  $0.73 \text{ kg ha}^{-1}\text{y}^{-1}$  (silver eels:  $0.25 \text{ kg ha}^{-1}\text{y}^{-1}$ ) for the entire river basin district (LLUR, 2008). Although both assessments estimated similar annual average catches per angler (LLUR, 2008:  $0.9 \text{ kg angler}^{-1}\text{y}^{-1}$ ; this study:  $0.84 \text{ kg angler}^{-1}\text{y}^{-1}$ ) the total catch differed largely. This indicates an underestimation of the number of active anglers in the present study which could be caused by the lack of catch data from anglers that are not organized in sport fishing clubs. However, according to the here presented results, a reduction of commercial and recreational eel fisheries provides a possible solution to substantially increase silver eel escapement from the Schwentine River.

Fisheries alone are not responsible for the reduced silver eel output. Natural mortality including predation must also be considered to have a considerable impact on silver eel production.



Sonntag et al. (unpublished data) reported that up to 4,000 great cormorants (*Phalacrocorax carbo*) were located in the area around the Schwentine River system in 2010. Stomach content analyses indicated that they consume around 1,200 kg eel per year ( $0.16 \text{ kg ha}^{-1}\text{y}^{-1}$ ). In proportion to fishery mortality this is only a minor fraction, but nonetheless it provides a factor for consideration.

Another threat for downstream migration silver eels are hydropower stations (Pedersen et al., 2012). In the present study it is striking that despite the provision of bypasses a considerable amount of eels was impinged in the trash rack and died. Almost the entire trash rack mortality during the three-year study period occurred during two migration peaks in November 2010 and 2011, where 70% and 77%, respectively of all downstream migrating silver eels were killed at the trash rack. During these periods the flap gate was closed. High mortality might have been caused by a combination of low water temperatures, increased river discharge and big amounts of incoming floating debris, which predominantly consisted of foliage that covered large areas of the trash rack and increased contact pressure at debris free areas. These results support previous observations of increased trash rack mortalities during periods of low water temperatures and high current velocities (Gosset et al., 2005), while the effect of floating debris has not yet been reported. During all other escapement events trash rack mortality remained very low and was only affecting single specimens. Trash rack mortality could be reduced considerably by short shutdown periods of hydropower stations during autumn, when river discharge is increased, water temperatures are low and floating foliage is present. Combined with an installation of bypasses with bottom entrances that fulfill eel specific requirements the escapement success of silver eels could be increased.

#### SILVER EEL QUALITY

In the Schwentine River fat content of all migrating silver eels exceeded 20% and appears to be above critical levels that might impair long swimming ability (Palstra et al., 2007; Van den Thillart et al., 2007). High *A. crassus* prevalences and infection intensities, however, provide matters of concern. While swim bladder damage was rather moderate in most individuals, also uninfected individuals showed effects of previous infections, which indicates that *A. crassus* prevalence might even exceed the here determined values. Severe *A. crassus* infection intensities were detected in approximately 21% of all analyzed individuals. It therefore must be considered that the number of escaping eels from the Schwentine River that successfully fulfill their spawning migration is reduced by another fifth since high infection intensities were shown to impair long

term swimming efficiency and potentially hinder eels from reaching the Sargasso Sea (Kirk, 2003; Palstra et al., 2007). This potential reproduction failure of a considerable fraction of escaping eels must be considered when implementing management measures and evaluating their benefit on silver eel escapement from river systems.

In summary, this study points out the importance of direct escapement assessments to provide reliable information on the silver eel production of a river system. It was shown that the Schwentine River provides a habitat, which delivers comparably little numbers of healthy spawners. It suffers from a lack of natural recruitment, high fishery mortality and a high abundance of *A. crassus*. In addition, three artificial barriers impair the downstream migration of escaping eels, two of which are hydropower stations that cause high mortalities. The number of eels reaching the river mouth must therefore be considered to be negligible. According to the here presented results the installation of fish protecting devices like bypasses and trash racks must be adjusted to eel specific requirements in order to minimize mortalities and migration disturbances at barriers. In addition, short term closures of fisheries and the shutdown of hydropower stations during particular environmental conditions would reduce silver eel mortality considerably. Although many factors influence the initiation of downstream migration, the observation of a few parameters and their implementation into management decisions seem to provide a realistic option to minimize silver eel mortalities during downstream migration and increase stock sustaining effects of management measures. Nevertheless, much effort is needed to reduce eel mortality, modify bypasses, improve habitat quality and reorganize restocking practice.

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# **CHAPTER II - Model Prediction versus Reality – Testing the predictions of a European eel (*Anguilla anguilla*) stock dynamics model against the *in situ* observation of silver eel escapement in compliance with the European Eel Regulation**

**E. Prigge<sup>1\*</sup>, L. Marohn<sup>1,3</sup>, R. Oeberst<sup>2</sup>, R. Hanel<sup>1,3</sup>**

<sup>1</sup>Helmholtz Centre for Ocean Research (GEOMAR), Duesternbrooker Weg 20, 24105 Kiel, Germany

<sup>2</sup>vTI - Institute for Baltic Fisheries, Alter Hafen Süd 2, 18069 Rostock, Germany

<sup>3</sup>vTI - Institute for Fisheries Ecology, Palmaille 9, 22767 Hamburg, Germany

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## **ABSTRACT**

A direct monitoring of European silver eel (*Anguilla anguilla*, L) escapement from rivers and estuaries has been proven to be challenging and a Europe-wide documentation of escaping silver eel numbers therefore seems hardly realistic. To reinforce management decisions, policy makers are thus widely reliant on the accuracy of escapement models. A 3-year program of silver eel escapement monitoring was undertaken to compile model input-data and revise an eel population model (German Eel Model II; GEM II) already used in the decision making process of management authorities. By compiling necessary input data and analyzing vital system-specific population characteristics it was possible to compare the documented silver eel escapement with the modeled potential silver eel escapement. Resulting model predictions were close to actually monitored escapement numbers, which were distinctly lower than reference escapement values for the same freshwater system given in the implementation report of the German Eel Management Plans. Applying different commercial and recreational catch scenarios documented the sensitivity of the model. Results document the potential of the GEM II and highlight the importance of high-quality input data to use model predictions as basis for management measures.

## INTRODUCTION

For centuries, the European eel (*Anguilla anguilla*, L) has been an important target species for fishers all over Europe (Tesch, 2003). However, since the 1980s, the stock has been in a steep decline and alarmingly low recruitment numbers are documented in virtually every time series available as well as reflected in landing numbers all over Europe (Dekker, 2003, ICES, 2010). Nowadays, the European eel stock is considered to be out of safe biological limits and the species is listed in Annex II of the Convention on International Trade in Endangered Species (CITES) (ICES, 2010). To stop the downward trend and support the recovery of the stock the European Council (EC) issued regulation No. 1100/2007 (European Union) on the 18th of September 2007 (European Union, 2007). One of its main objectives is to guarantee a minimum of a 40% spawner escapement to the sea in relation to the potential spawner escapement under pristine conditions. Each EU member state was obliged to elaborate Eel Management Plans (EMP) on a river basin level to reach the given escapement target. A rejection of the EMP would entail strict reductions and eventually the closure of the national eel fisheries.

Therefore, a proper evaluation of any management measure implies the assessment of silver eel spawner escapement, which is methodologically challenging, especially for large river systems. Recent attempts have been largely based on commercial landings (Charrier et al., 2012), sonar-based quantification (Bilotta et al., 2011), mark-recapture studies or estimations derived from tagging experiments (Amilhat et al., 2008, Feunteun et al., 2000) as well as the application of stock and escapement models (Aprahamian et al., 2007, Bevacqua et al., 2007, Fenske et al., 2011), reviewed by De Leo et al. (2009).

As a panmictic species, the European eel lacks a well defined population structure (Als et al., 2011). Fenske et al. (2011) pointed out for *Anguilla rostrata* that a common spawning ground and overlapping generations likely lead to a situation where local recruitment is not directly related to overall stock size or local spawner abundance. This also holds true for the closely related European eel. Most common fish population models have been developed for iteroparous species with well defined population structures. To take this into account, models estimating population dynamics in eel are often trying to cover large geographical scales and are therefore largely dependent on input data compiled from literature sources (Aprahamian et al., 2007, Åström and Dekker, 2007, Lambert and Rochard, 2007). Thus, in the absence of system-specific input data, it is often necessary to convert and generalize vital population characteristics onto a larger scale and/or simplify the model assumptions (Aprahamian et al., 2007, Åström and Dekker, 2007). It has however been shown for several Anguillidae species (including the European eel) that vital population characteristics differ with system and/or habitat (Jessop,

2010, Lin et al., 2007, Melia et al., 2006, Poole and Reynolds, 1998, Vøllestad, 1992). Therefore, generalizations can significantly bias the model outcome and limit the conclusiveness of model-based management measures.

Factors influencing the actual amount of escaping silver eels from freshwater systems into coastal waters are numerous and widely discussed (Arahamian et al., 2007, ICES, 2010). They range from commercial and recreational fishing over predation by birds (e.g. cormorants) to migration barriers (ICES, 2010). Additionally, to evaluate the influence of each factor, initial recruitment numbers, e.g. stocking and/or natural immigration of juveniles to a freshwater system, are of high importance. In order to estimate the dynamics of the European eel stock with respect to immigration, restocking, natural mortality, mortality caused by commercial and recreational fisheries, predators (such as cormorants) and hydropower turbines, Oeberst and Fladung (2012) developed an age-structured eel population model for the River Elbe system (Germany) – the GEM II. One of the main output parameters of this model is the amount of silver eels that are potentially able to migrate out of a specific system. The main advantage of the model is the possibility to account for uncertainties of the source data, as e.g. data on immigrating eels is often only available in poor quality.

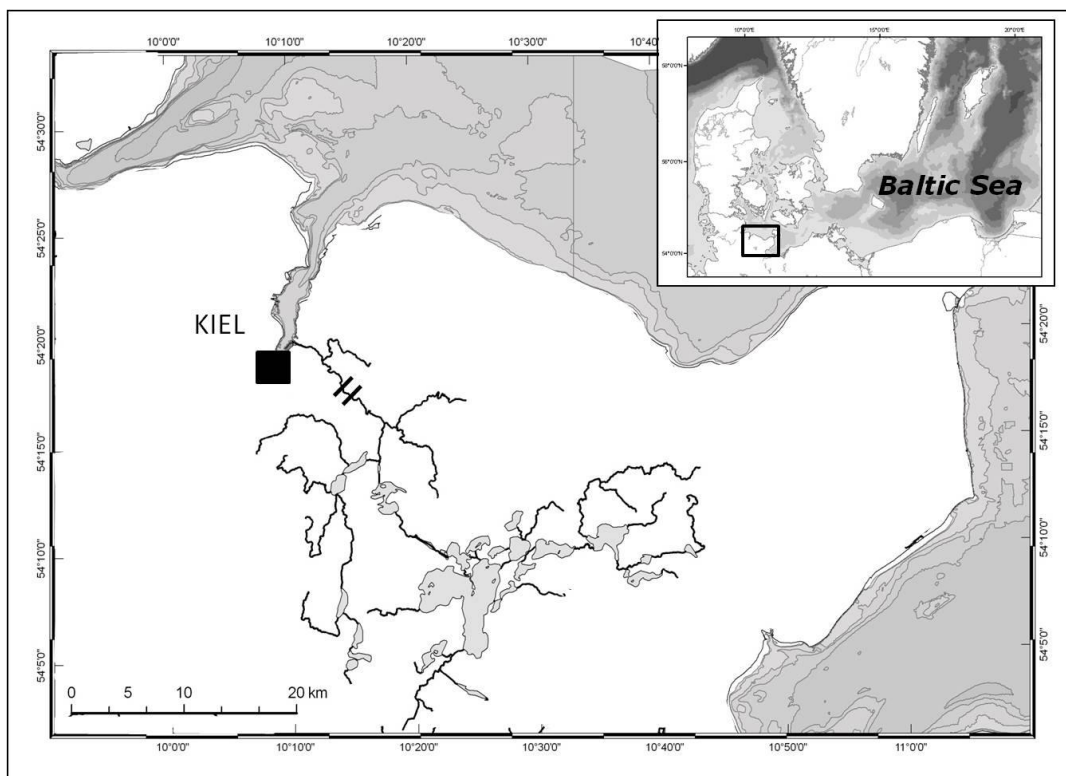
In order to evaluate models directly used in the decision making process of management authorities, it is important to ensure detailed and continuous system-specific data time series. The advantage of the Schwentine River system monitored in the present study is the absence of any natural immigration of eels (eliminating an input factor often hard to grasp), the relatively high quality of model input data due to its limited size, and relatively small number of stakeholders as well as the possibility to directly monitor the actual silver eel escapement, thereby allowing a comparison of different management scenarios.

The study objective was to compare predicted silver eel escapement of the eel population model described by Oeberst and Fladung (2012) with the direct count of escaping silver eels. Thereby, the potential of eel population modeling in supporting the decision making process of management authorities should be evaluated.

## MATERIAL AND METHODS

### STUDY AREA

The Schwentine River system (part of the Schlei-Trave river basin district) close to Kiel was chosen as an exemplary freshwater system to monitor actual silver eel escapement and collect necessary model input data (Figure II-1). The system consists of several freshwater lakes connected by the Schwentine River and has a total area of approximately 7500 ha (total area of lakes: 5984 ha). It discharges into the Kiel Fjord (54°19'39"N 10°11'11"E) with an average discharge of  $3.9 \text{ m}^3 \text{ s}^{-1}$  and ranging from approximately  $0.6 \text{ m}^3 \text{ s}^{-1}$  to  $13.4 \text{ m}^3 \text{ s}^{-1}$ . It has been blocked for any upstream fish migration for more than 100 years by two consecutive hydropower stations approximately 7 km and 9 km upstream the river mouth. Since 2005 the upper hydropower station ("Raisdorf II") is equipped with a fish pass combined with trash-racks (light spacing: 20 mm) in front of the turbine entries allowing up- and downstream migration of fish. All silver eels leaving the system are forced to use the fish pass and end up in a fish trap. Up to date, the lower hydropower station is still not equipped with a fish pass and thus, no natural ascent of juvenile eels into the system is possible. Therefore, the entire local eel population depends on stocking conducted by commercial fishermen, angling societies and government authorities.



**FIGURE II-1** Study area: Schwentine River system in northern Germany, discharging into the Baltic Sea. Inset shows location of study area in the Baltic Sea area. Black bars in the main map indicate hydropower stations.

## MODEL DESCRIPTION

The GEM II, developed by Oeberst and Fladung (2012), is an age-structured population model describing eel stock dynamics and estimating the potential escaping silver eel escapement both in numbers and total weight. Escapement is predicted based on vital population characteristics, immigration (including stocking), natural mortality and mortalities caused by recreational/commercial fisheries, cormorants and hydropower (Oeberst and Fladung, 2012). Cormorant predation was considered separately to better incorporate the highly variable effect of bird predation in distinct freshwater systems (Oeberst and Fladung, 2012). Even though this model has been developed to document eel stock dynamics in the Elbe river, it is not limited to it and can be transferred to other freshwater systems. Developed in 2008 the model was subsequently adapted according to new data and literature information to meet the requirements of the implementation report of the German EMPs in 2012 (Oeberst and Fladung, 2012) and was part of the EU project “Pilot projects to estimate potential and actual escapement of silver eel” (POSE, Walker et al., 2011).

The GEM II used here was restricted to 20 age classes, because age reading resulted in only a negligible number of eels older than 20 years. Therefore, it was assumed that eels rarely stay longer than 20 years in the Schwentine River system. Availability of data dramatically decreased prior to the early 1990s and time horizon for the model had to be set to 17 years (1993-2010). This time frame, however, was considered to sufficiently minimize the bias introduced by using a dummy start population and compare calculated with actually monitored escapement in the years 2009 and 2010. It was therefore necessary to compile model input data stretching back to the year 1993. For a detailed description of the GEM II see Oeberst and Fladung (2012).

The GEM II allows integrating mortalities caused by hydropower plants. In the Schwentine River systems, two hydropower plants impede the escapement of silver eels (Figure II-1). However, since escapement numbers were assessed at the upper hydropower plant and trash racks were regularly checked for eels, hydropower mortality was set to be zero in the present study. Furthermore, the model was restricted to a total wetted area of 5984 ha. The often small rivers connecting the systems' lakes were negligible, because fishing as well as stocking activities are mainly restricted to lake habitats.



## DATA COLLECTION

A 3-year silver eel monitoring program was initiated to collect system-specific model input data and escapement numbers of the Schwentine river system. Monitoring of silver eel escapement out of the Schwentine River in the years 2009 and 2010 was performed by regular inspection of a trap blocking the fish pass that bypasses the upper hydropower station. Total length, wet mass, eye diameter and pectoral fin length of every single eel caught was documented and eels were assigned to a maturity stage according to Durif et al. (2005). To reinforce data collected at the fish trap and prevent biasing the assessment of system-specific vital population characteristics (e.g. length-weight relation) towards migrating eels leaving the system, commercial catches were analyzed for length-weight relationship and proportion of silver eels (subsample) once a month in each summer. In total, 147 eels (total length spectrum: 20.2 – 102.5 cm) were measured to determine the length-at-age relationship for the Schwentine river system. Otoliths were prepared and read according to the manual published by the “ICES Workshop on Age reading of European and American Eel” (ICES, 2009).

Since natural recruitment was considered to be zero in the Schwentine River system, recruitment numbers equal stocking numbers. Stocking with eel is decentralized in Germany and respective data (1993-2010) were collected from local state authorities (State Agency for Agriculture, Environment and Rural Areas, LLUR) as well as fishers and angling societies operating in the Schwentine River system. Numbers of stocked eels were provided in total weight [kg] per year and respective water body within the system and (when possible) subclassified in “glass eels”, “elvers” and “yellow eels”. Total stocking in kg was transferred to numbers based on the average weight of different estimated age-groups and varied between approximately 238 000 and 13 500 individuals per year.

Commercial catch data were provided by the LLUR. Data were cross-checked and if possible amended by data from the individual fishers. In case no catch data were available for individual lakes and single years, gabs were filled according to yearly over-all average catch per hectare. Catch data were provided in total weight [kg] per year and respective water body. Minimum legal size of eels in the Schwentine River system is 35 cm for both commercial and recreational fishers. However, local fishermen communicated that eels of this size are usually too small to be put on the market and actual minimal landing size was assumed to be 50 cm. Since recreational catch data were not collected in a centralized data base, historical catch data of two of the biggest angling societies located in the Schwentine area were analyzed to estimate an average catch [kg] of eel per angler and year. The average catch was then multiplied by the total number of recreational fishers in the Schwentine River system per year.

As the cormorant (*Phalacrocorax carbo*) is often regarded as one of the major predators on eel in European freshwater systems, bird predation was separately assessed by stomach content analysis and analysis of regurgitant samples collected in the central colony of the Schwentine River System. Cormorants shot by entitled fishermen were collected and stored frozen at -40°C for subsequent stomach content analysis. Stomach contents were screened for otoliths and other remains of *A.anguilla*. Regurgitant samples were collected during daytime once a month and stored frozen at -20°C prior to analysis. In addition, total cormorant numbers (residents and migrants) were counted. Retrospective cormorant predation on eel was modeled using a time series of cormorant numbers (2000-2010) for the Schwentine River system and an energetic consumption model according to Tasker and Furness (1996) (N. Sonntag, unpublished). Cormorant predation for the years 2000 to 2010 was estimated to range between 700 and 1 800 kg. Due to a lack of information on the cormorant numbers prior to the year 2000 the cormorant predation assessed by Worthmann and Spratte (1987) for the year 1987 (1 187 kg) was used as a constant for 1993-1999.

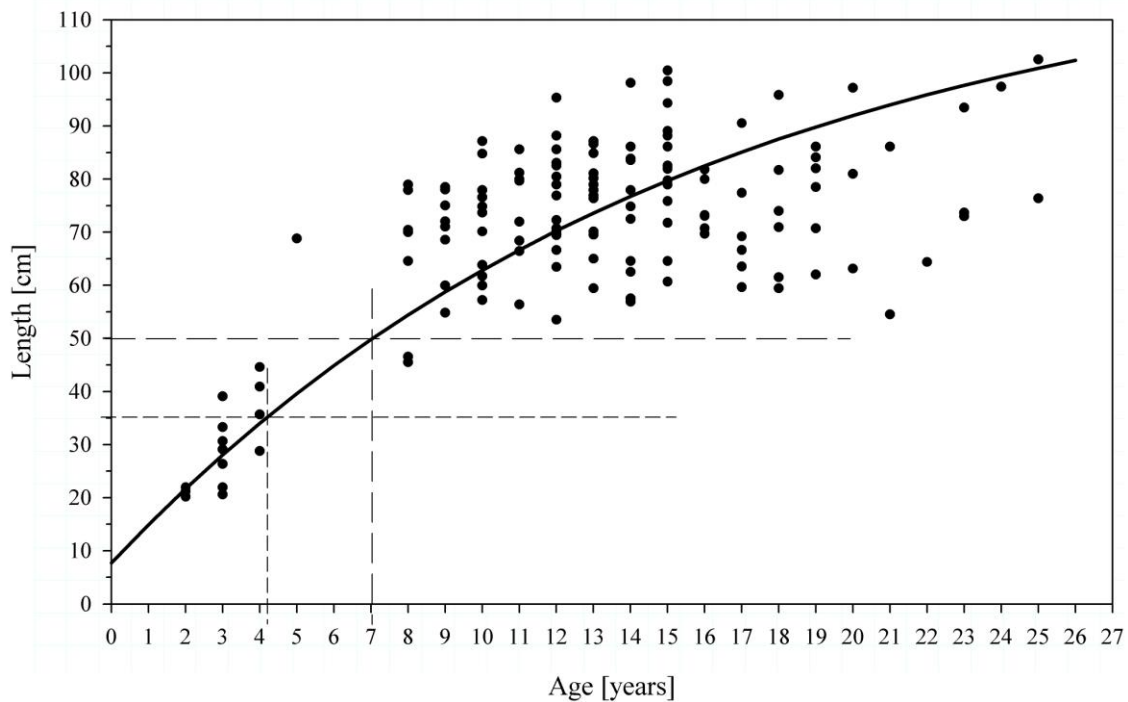
#### VITAL POPULATION CHARACTERISTICS

The GEM II requires several system-specific, age- or size-structured population characteristics to describe the local stock dynamics. Growth rates of European eels are highly variable with habitat and sex (Poole and Reynolds, 1996, Svedäng et al., 1996, Melia et al., 2006). Due to the relatively small size-at-maturity of male European eels (Tesch, 2003) it was not possible to quantitatively sample them in the fish trap. Monitoring results and model estimations are, therefore, restricted to female European eels in the Schwentine River system. System-specific eel growth of females was described using the von Bertalanffy growth function (VBGF):

$$L_t = L_{\infty} [1 - e^{-K(t-t_0)}] \quad (1)$$

where  $L_t$  is the length at time  $t$ ,  $L_{\infty}$  the asymptotic length,  $K$  the growth coefficient and  $t_0$  the initial condition parameter when the hypothetical length is zero. Fish growth is commonly described by the VBGF with all three parameters being based on length-at-age data (Chen et al., 1992). It has, however, been questioned whether the VBGF is actually capable of describing the growth in eels (Sparre, 1979). To account for uncertainties of the VBGF in estimating the growth of semelparous fish species Froese and Pauly (in press) suggest setting the asymptotic length ( $L_{\infty}$ ) to a fixed value. Semelparous fish are expected to mature at the size and age of maximum growth rate in weight to maximize their expected reproductive output (Froese and Pauly, in

press) and Froese and Pauly (in press) expect one-time spawners to mature slightly before reaching 0.67 asymptotic length ( $L_{\infty}$ ). Accordingly and since more precise values are missing for eels, the average length of escaping silver eels (83.1 cm,  $N = 357$ , subsample of stage F IV and F V eels) was considered to constitute approximately 2/3 (66%) of the system-specific  $L_{\infty}$ . Therefore,  $L_{\infty}$  was set to  $83.1 \text{ cm} / 0.66 = 124.6 \text{ cm}$ . Additionally,  $t_0$  was set to -1 in order for the VBGF to describe the length of age class 0 between 60 and 75 mm, the length associated with the zero band in otoliths of glass eels arriving at the European continent and thus entering the continental growth phase (Poole et al., 2004, ICES, 2009b, Daverat et al., 2012). Estimation of  $k$  based on length-at-age data of 147 eels (silver eels, yellow eels and juveniles) with  $L_{\infty}$  and  $t_0$  fixed resulted in 0.0638 and was calculated in STATISTICA 8.0 (StatSoft Inc.). VBGF used in the GEM II and documented length-at-age of sampled eels are given in Figure II-2.



**FIGURE II-2** von Bertalanffy growth function (VBGF) for European eel in the Schwentine River system. Horizontal line indicates legal minimal landing size (35 cm) of *A.anguilla* for commercial fishermen and angling societies and actual minimal landing size (50 cm) after personal communication with fishermen.

The age at a given length was estimated according to (Oeberst and Fladung, 2012):

$$\alpha' = t_0 - LN\left(1 - \frac{L}{L_{\infty}}\right) / k \quad (2)$$

$$a = \text{round}(\alpha') \quad \text{with } \alpha' \text{ rounded to the closest integer} \quad (3)$$

System-specific mean weight by age group was estimated based on the weight-at-length relationship  $W = a \cdot L^b$  ( $a = 0.0012$  and  $b = 3.1106$ ) in combination with Equations 2 and 3. The regression parameters  $a$  and  $b$  were estimated using weight and length data of 518 eels sampled in the fish pass and from commercial catches (length range: 32.5 – 100.7 cm; weight range: 62.4 – 2249.7 g). All length based data were then transferred into age based data by combining (2) and (3).

System-specific sexual maturity (fraction of silver eels) was assessed as proportion of mature females per age class. The fraction of silver eels per age class was described by fitting a logistic model to maturity data (silver stage according to Durif et al., 2005) from female eels ( $N = 640$ ) collected in the Schwentine River system.

Natural mortality was included according to the model of Bevacqua et al. (2011). The model estimates the proportion of eels that died from natural causes per age class based on the mean water temperature of the system, the density of the eels (three possible density levels) and the system specific length-weight-relationship. As small changes in temperature lead to significant changes in natural mortality, a temperature time series (provided by the LLUR) was used to model natural mortality on a yearly basis retrospective to 1993. With respect to the stocking numbers assessed for the model period, system-specific eel density was considered to be high.

#### PARAMETER FITTING AND MODEL SCENARIOS

While most of the parameters were directly assessed by sampling data on eels in the Schwentine River system (length-at-age, age-at-maturity, etc.), it was necessary to artificially estimate the dummy start population. The age-distribution of the start-population (1993) was estimated based on the years 2002-2004. It strongly influences the age distribution and stock abundance of the first model years with decreasing effects during the following model period (Oeberst and Fladung, 2012). The start population can be further adjusted to presumable stocking activities prior to 1993 by introducing an additional factor ('factor for year one'). The "factor for year one" influences the age distribution of the first model year compared to the reference period for the dummy start population. Setting this factor  $> 1$  indicates a higher stocking prior to 1993

compared to the following years. Contrastingly, values  $< 1$  indicate lower stocking prior to 1993. In addition, the fraction of silver eels per age class can be corrected for large yellow eels otherwise not accounted for by the logistic model. This can be done by varying the maximum proportion of yellow eels that transfer to silver eels ( $F_B \leq 1$ ). Changing  $F_B$  strongly influences the age distribution of potentially emigrating silver eels. Values approaching 1 for  $F_B$  will result in relatively young silver eels leaving the system, while decreasing  $F_B$  increases the number of older silver eels (Oeberst and Fladung, 2012). These two parameters can be varied to achieve the best possible structural agreement between model outcome and field data and thereby to identify the best performing model variant. To avoid the unintentional leveling of predicted and documented escapement numbers, parameter fitting was based on the comparison of modeled and documented relative age distribution instead of absolute numbers. To achieve frequencies  $> 5$  necessary for the statistical analysis, existing 20 age classes were grouped as 4 age groups. Absolute numbers of potentially escaping silver eels (based on the GEM II) were normalized to monitoring numbers. Goodness of fit between observed and predicted relative age distributions of silver eels was tested by chi-square test (MS EXCEL).

To document the sensitivity of the model several model scenarios were run, once the best performing model variant was identified. Scenarios included the reduction and increase of commercial and recreational fisheries by 10% and the reduction and increase of stocking by 10%. In all scenarios only the respective input parameter was changed while the remaining set of input parameters stayed the same as in the best performing model variant.

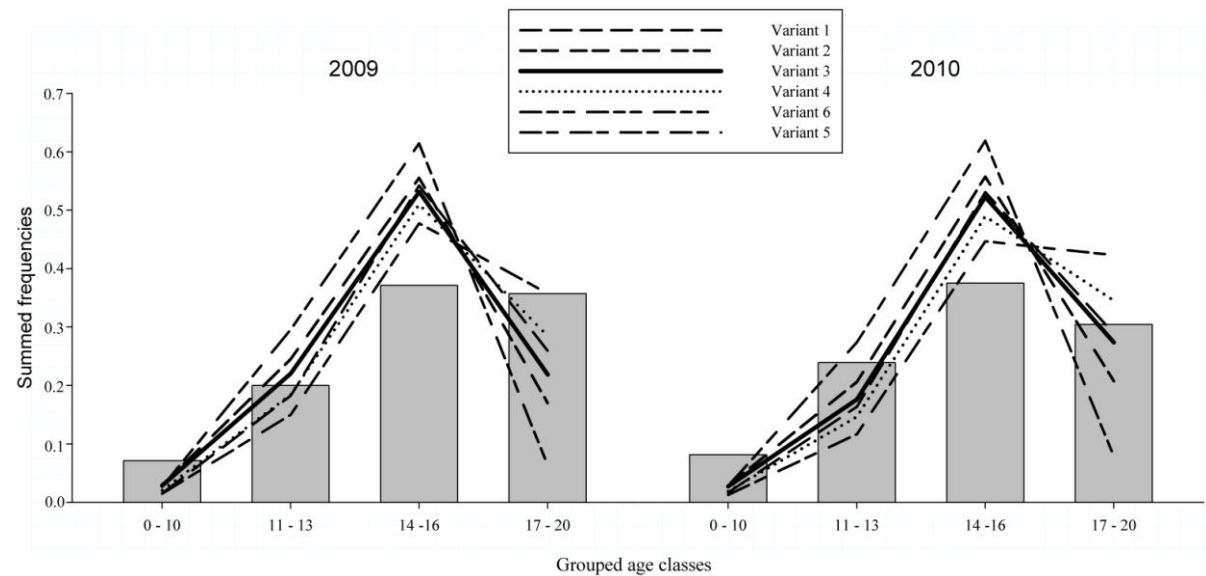
## **RESULTS**

Relative age distribution (based on the GEM II) of potentially escaping silver eels from the Schwentine River system was strongly influenced by changes in  $F_B$  and 'factor for year one', while resulting changes in absolute numbers were relatively small. It was not possible to adjust the parameters in a way that relative age distribution of GEM II variant and monitoring results matched beyond doubt. Chi-square goodness of fit analysis resulted in significant differences between the observed and expected relative age distribution of escaping silver eels for 2009 and 2010 in all model variants. Chi-square-test results of varying  $F_B$  and 'factor for year one' are given in Table II-1.

**TABLE II-1 Model variants tested to identify the best performing setting of  $F_B$  and “factor for year one”. All variants were run with the same set of assessed input parameters while changing  $F_B$  and “factor for year one” accordingly to the values given here. Goodness-of-fit analysis ( $\chi^2$ -test) was done comparing the relative age distribution of predicted and documented silver eel escapement.  $\chi^2$ -test identified Variant 3 (highlighted) to represent the best fit.**

	Variant 1	Variant 2	Variant 3	Variant 4	Variant 5	Variant 6
factor for year one	1	0.5	<b>0.4</b>	0.4	0.4	2
$F_B$	1	0.5	<b>0.3</b>	0.2	0.1	1
<i>df</i>	3	3	<b>3</b>	3	3	3
$\chi^2$ test (year 2009)	20.40	23.54	<b>14.06</b>	12.54	17.41	109.90
$\chi^2$ test (year 2010)	60.89	38.13	<b>32.26</b>	54.26	96.53	155.64
critical value $\chi^2$ distribution ( <i>df</i> = 3, <i>p</i> = 0.05)	7.81	7.81	<b>7.81</b>	7.81	7.81	7.81

Observed and predicted relative age distributions for the years 2009 and 2010 and varying GEM II variants are given in Figure II-3. To compare absolute numbers of actually escaping silver eels (monitoring 2009 and 2010) and potentially escaping silver eels estimated by the GEM II, the model variant with the smallest sum of chi-square-test values (variant 3;  $F_B=0.3$  and ‘factor for year one’ = 0.4) was used.



**FIGURE II-3 Relative frequency distribution of grouped age classes (2009 and 2010) of actually escaping silver eels (grey bars) and potentially escaping silver eel from different model variants (varying lines).**

Yearly stocking with *A. anguilla* of different age classes ranged from approximately 13 500 (2008) to 238 000 (1993) individuals. The local eel biomass in the Schwentine River system was estimated (GEM II) at 24 981 kg (85 695 eels) in 2009 and 21 123 kg (119 633 eels) in 2010 (Table II-2). Directly assessed commercial landings summed up to a total of 5 233 kg in 2009 and 6 610 kg in 2010. The GEM II estimated the according absolute numbers to be 9 486 eels in 2009 and 13 690 eels in 2010 (Table II-2). Calculated recreational landings amounted to 830 kg both in 2009 and 2010. Cormorant predation was assessed to be 1 100 kg in 2009 and 1 200 kg in 2010. The GEM II estimated the according absolute numbers to be 10 680 eels in 2009 and 11 650 eels in 2010 (Table II-2).

TABLE II-2 A. *anguilla* stock size, mortalities and potentially escaping silver eels for the Schwentine River system for 2009 and 2010, estimated by the GEM II (variant 3). Numbers in brackets indicate the respective percentage with respect to the total stock size of the same year.

	2009				2010			
	[kg]		[eels]		[kg]		[eels]	
stock size	24981		85695		21123		119633	
natural mortality	2267	(9.1)	12193	(14.2)	2120	(10.0)	21648	(18.1)
commercial fishermen	5233	(20.9)	9486	(11.1)	6610	(31.3)	13690	(11.4)
recreational fishermen	830	(3.3)	1505	(1.8)	830	(3.9)	1720	(1.4)
cormorant	1100	(4.4)	10680	(12.5)	1200	(5.7)	11650	(9.7)
<b>silver eels</b>	<b>748</b>	<b>(3.0)</b>	<b>728</b>	<b>(0.8)</b>	<b>385</b>	<b>(1.8)</b>	<b>363</b>	<b>(0.3)</b>
	[kg/ha]		[eels/ha]		[kg/ha]		[eels/ha]	
commercial fishermen	0.9		1.6		1.1		2.3	
recreational fishermen	0.1		0.3		0.1		0.3	
cormorant	0.2		1.8		0.2		1.9	
<b>silver eels</b>	<b>0.13</b>		<b>0.12</b>		<b>0.06</b>		<b>0.06</b>	

Silver eel monitoring at the hydropower station (2009 and 2010) resulted in unexpected low escapement numbers of female silver eels. In 2009 only 133 silver eels were documented with a total weight of 144 kilos resulting in  $0.02 \text{ kg ha}^{-1} \text{ y}^{-1}$  (total area accounted for: 5984 ha). In 2010 the total number of emigrating silver eels was 683 with a total weight of 691 kilos resulting in  $0.12 \text{ kg ha}^{-1} \text{ y}^{-1}$  (total area accounted for: 5984 ha). Potential silver eel escapement numbers estimated by the GEM II slightly differed from monitoring results. The model calculated 728 silver eels (748 kg) for 2009 and 363 silver eels (385 kg) for 2010 corresponding to  $0.13 \text{ kg ha}^{-1} \text{ y}^{-1}$  in 2009 and  $0.06 \text{ kg ha}^{-1} \text{ y}^{-1}$  in 2010 (Table II-2 + II-3).

TABLE II-3 Silver eel output for fishermen/angler scenarios, reference estimate and 40% aim for the Schwentine River system.

Scenario	2009		2010	
	kg ha <sup>-1</sup> y <sup>-1</sup>	stck ha <sup>-1</sup> y <sup>-1</sup>	kg ha <sup>-1</sup> y <sup>-1</sup>	stck ha <sup>-1</sup> y <sup>-1</sup>
reference estimate*	1.5 - 3.8 kg ha <sup>-1</sup> y <sup>-1</sup>			
40% aim**	0.6 - 1.52 kg ha <sup>-1</sup> y <sup>-1</sup>			
<b>original</b>	<b>0.13</b>	<b>0.12</b>	<b>0.06</b>	<b>0.06</b>
fishermen -10%	0.34	0.33	0.29	0.26
fishermen +10%	0.01	0.01	0.04	0.05
angler -10%	0.16	0.16	0.10	0.09
angler +10%	0.09	0.09	0.03	0.03

\* Anonymous (2012)

\*\* Escapement aim formulated by the EU

Reducing the catch numbers of the commercial fisheries by 10% (“fishermen -10% scenario”) resulted in 1 948 potentially escaping silver eels (2 044kg) in 2009 and 1 579 silver eels (1 709 kg) in 2010 (Figure II-4).

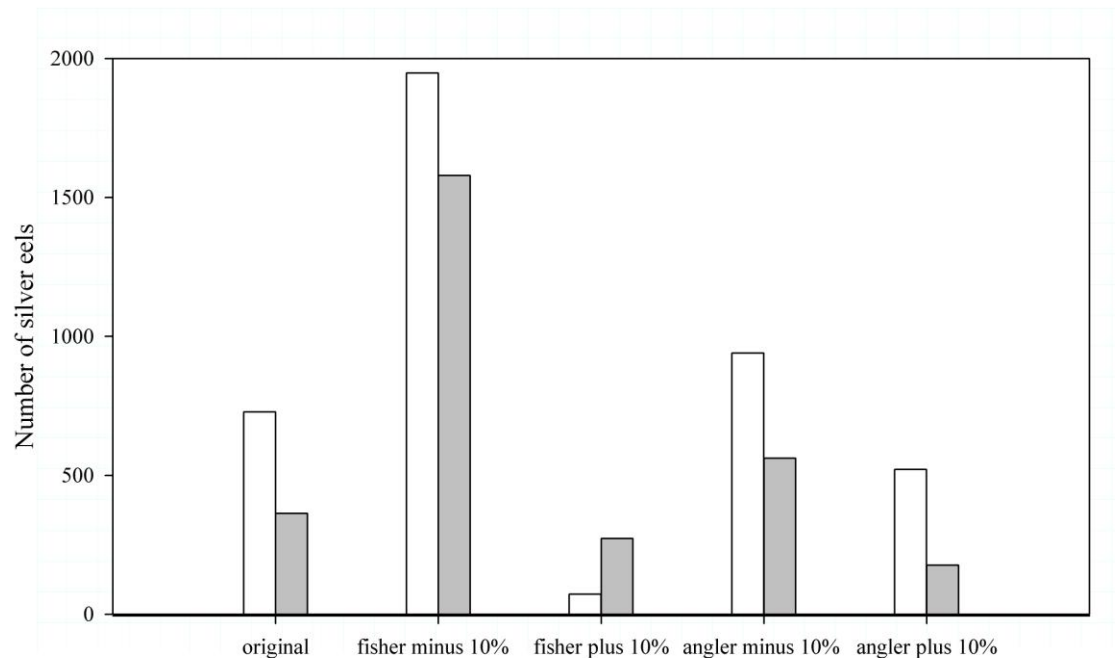


FIGURE II-4 Number of potentially escaping silver eels for 2009 (light bars) and 2010 (black bars) with different fishery scenarios



The “fishermen -10% scenario” resulted in a ~ 168% increase of the number of escaping silver eels for 2009 and a ~ 335% increase for 2010. Increasing the catch numbers of the commercial fisheries by 10% (“fishermen +10% scenario”) resulted in 72 silver eels (63 kg) in 2009 and 273 silver eels (259 kg) in 2010 (Figure II-4). The “fishermen +10% scenario” resulted in a ~ 90% decrease of silver eels numbers for 2009 and a ~ 25% decrease for 2010. Reducing the catch numbers of the recreational fisheries by 10% (“angler -10% scenario”) resulted in 940 potentially escaping silver eels (970 kg) in 2009 and 562 silver eels (599 kg) in 2010 (Figure II-4). The “angler -10% scenario” resulted in a ~ 29% increase of silver eels numbers for 2009 and a ~ 45% increase for 2010. Increasing the catch numbers of the recreational fisheries by 10% (“angler +10% scenario”) resulted in 521 silver eels (533 kg) in 2009 and 177 silver eels (188 kg) in 2010 (Figure II-4). The “angler +10% scenario” resulted in a ~ 28% decrease of silver eels numbers for 2009 and a ~ 51% decrease for 2010. Silver eel output for different scenarios is summarized in Table II-3.

## DISCUSSION

Estimated potential silver eel escapement based on the GEM II output was at about the same level as the directly monitored escapement of silver eels out of the Schwentine River system. However, it has to be highlighted that the GEM II, besides describing the dynamics of the eel stock, estimates the potential silver eel escapement, namely the number of eels that become silver and potentially could start their migration out of the system. It has, however, been shown that the actual amount of silver eels starting their migration is strongly influenced by environmental parameters and obstacles (Acou et al., 2008, Breteler et al., 2007, Feunteun et al., 2000, Vøllestad et al., 1986) indicating that silver eels despite an advanced maturity stage might postpone the onset of migration and even reverse to the yellow stage when facing unfavorable conditions (Durif et al., 2003, Durif et al., 2005).

The age-structured GEM II requires length-based data to be transferred into age-based data. Therefore, the growth function used to transfer length-based data into age-based data strongly influenced the necessary input data and thus had a large influence on the model outcome. Eel growth is highly dependent on habitat (Svedäng et al., 1996, Melia et al., 2006) and published growth functions for female *A. anguilla* vary significantly (De Leo and Gatto, 1995, Holmgren et al., 1997, Poole and Reynolds, 1996, Simon, 2007). Describing eel growth, in general, has been proven to be challenging and Sparre (1979) even suggested renouncing the use of VBGF. Nevertheless, VBGF was used to describe the growth of eels in the original GEM II (Oeberst and

Fladung, 2012) and to document the models' potential also in the present model variant. In the present study, fixing the  $L_{\infty}$  at 1.5 times the average size of escaping silver eels accounted for system-specific maturation patterns. The resulting VBGF closely resembled both the documented system-specific length-at-age relation and the VBGF ( $L_{\infty} = 114$  cm,  $K = 0.058$  and  $t_0 = -0.81$ ) for eels in the Schwentine River system previously given by Worthmann and Spratte (1987). The high plasticity of growth in eels causes enormous variation not only between habitats, but also between sexes (Poole and Reynolds, 1996) and a sensible growth description usually requires two individual VBGF for females and males, respectively (Melia et al., 2006, Poole and Reynolds, 1996). As it was not possible to catch enough males in the Schwentine River System to allow a sound analysis, the present VBGF and the GEM II were restricted to females. Sex determination in freshwater eels is believed to be environmentally induced and eels enter freshwater as sexually undifferentiated glass eels (Davey and Jellyman, 2005, Holmgren and Mosegaard, 1996, Wiberg, 1983). Besides population density and habitat quality, geographical habitat differences have been proposed to influence the sex ratio of European eels (Tesch, 2003, Kettle et al., 2011). Tesch (2003) and Kettle et al. (2011) described northern European waters to predominantly favor female dominated populations, while southern European waters may support eel populations strongly skewed towards males. Stocking numbers and available habitat area in the Schwentine River system implicated a relatively high population density and natural mortality was calculated appropriately. It has been proposed that high population densities relative to available habitat area and quality result in male-dominated sex ratios (Krueger and Oliveira, 1999). Due to the relatively small size of male European eel (Tesch, 2003), the monitoring in the present study was probably biased towards females. However, legal minimum catch size for the European eel and according mesh sizes in the commercial fishery should have been able to document a male dominated population in the Schwentine River system. In addition, Wickström et al. (1996) showed that juvenile eels stocked into northern European freshwater systems with limited natural recruitment predominately develop into females. They estimated that in a lake with even higher stocking densities than in the Schwentine River System, only approximately 3.4% of stocked elvers and glass eels developed to males (Wickström et al., 1996). Present catch composition of commercial fishermen and escapement monitoring results confirmed an eel population in the Schwentine River system dominated by females and the male bias was considered to be negligible.

In spite of the absence of a Baltic Sea glass eel time-series, natural glass eel recruitment to Baltic Sea tributaries is commonly believed to be low (ICES, 2011, Westerberg, 1998). Generally low recruitment combined with the still existent blockage of any upstream migration into the

Schwentine River system by two consecutive hydropower station support the idea of a local occurrence of eel being entirely dependent on stocking. Additionally, Prigge et al. (2013) showed that at least 62.5% of silver eels emigrating from the Schwentine River system had otolith Strontium to Calcium ratio profiles consistent with an individual stocking history. Stocking numbers provided by commercial fishermen, recreational angling societies and state authorities were therefore considered to represent the entire recruitment of juveniles to the Schwentine River eel population.

While the cumulated catch data for the commercial fishery were directly provided by commercial fishers and legal authorities, the effect of recreational fishermen had to be estimated from average catch and total amount of anglers in the Schwentine River system. The generalization of individual preferences and target species in angling most likely led to a loss in data quality. In addition, it was not possible to account for anglers who are not organized in angling societies in the Schwentine River system and total recreational catch numbers used in the current GEM II variant are most likely underestimated. It has previously been reported that on average recreational fishermen in Germany land about 0.65 kg of eel per year (Anonymous, 2012). Calculated average catch in the Schwentine River system was slightly higher (approximately 0.9 kg per recreational fishermen and year) (L. Marohn, unpublished). Therefore, the underestimation of the total number of recreational fishermen might be balanced by an overestimation of the average catch.

The milestone report (Anonymous, 2012) of the implementation of the German EMP estimates the pristine reference silver eel escapement of the Schlei-Trave river basin (discharging into the Baltic Sea) between 1.5 and 3.8 kg ha<sup>-1</sup> y<sup>-1</sup>. The 40% minimum escapement postulated by the EU (European Union, 2007) would therefore require an escapement between 0.6 and 1.52 kg ha<sup>-1</sup> y<sup>-1</sup>. Potential escapement based on the GEM II for 2009 and 2010 was thus at about 10 to 21% of the lower 40% escapement aim (0.6 kg ha<sup>-1</sup> y<sup>-1</sup>). Connecting rivers in the Schwentine System are usually rather shallow and fast flowing while Laffaille et al. (2003) showed that larger eels tend to prefer deeper freshwater habitats. In addition, stocking and eel fisheries in the Schwentine River system outside the lake habitats are negligible. Consequently, uncertainties in estimated eel population dynamics due to area-restriction of the GEM II were considered to be negligible as well.

Different eel fisheries scenarios showed that estimates of potential escapement are strongly dependent on input data. Changing the number of eels taken by commercial and recreational fisheries by only 10% significantly influenced the number of potentially escaping silver eels. Legal restrictions of the commercial/recreational eel fisheries, however, seem to be one of the

possible measures showing instant short-term improvement of escapement numbers, but concurrently are often subject of great public controversies (Dorow and Arlinghaus, 2012). Due to the retrospective construction of the different scenarios, however, implications for system-specific management decision are limited.

The present study constitutes one of the first to actually compare the silver eel escapement of a small freshwater system with the potential escapement predicted by an escapement model. Even though the Schwentine River system has to be considered a small to medium freshwater system and number of involved stakeholders is limited, compiling the necessary input data and characterizing the vital population characteristics was challenging. Nevertheless, results document the potential of the GEM II when estimating escaping silver eels in numbers and weight. At the same time, present results highlight the importance of high-quality data bases to secure a sound model-based management and question the compliance of regional management strategies with the minimum criteria defined by the European eel regulation.

## **ACKNOWLEDGMENTS**

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## CHAPTER III - Tracking the migratory success of stocked European eels (*Anguilla anguilla*) in the Baltic Sea

E. Prigge<sup>1</sup>, L. Marohn<sup>1,2</sup>, R. Hanel<sup>1,2</sup>

<sup>1</sup>Helmholtz Centre for Ocean Research (GEOMAR), Duesternbrooker Weg 20, 24105 Kiel, Germany

<sup>2</sup>vTI - Institute for Fisheries Ecology, Palmaille 9, 22767 Hamburg, Germany

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### ABSTRACT

It is still under debate to what extent European silver eels (*Anguilla anguilla*) that originate from stocking programs in the Baltic Sea tributaries can effectively contribute to the spawning stock. To address this question we tagged 274 formerly stocked European eels emigrating from the Schwentine River near Kiel (Germany) with T-bar anchor tags. A total of 29 eels were reported recaptured (approx. 11%) up to 14 months after release. Recapture locations concentrated around the outlet of the Baltic Sea (Danish Belt Sea) with 62% of all recaptures reported here or in the Kattegat. Recaptured eels showed a reduction in both length and mass ( $-1.5 \pm 0.9$  cm and  $-125.3 \pm 50.1$  g) while average total fat content was still  $28.4 \pm 4.4\%$  which is in the order of values previously reported to be high enough to provide energy resources to successfully complete the spawning migration. However, documented mean rate of travel ( $0.8 \text{ km day}^{-1}$ ) indicates a delay of a target-oriented migration and might be interpreted as delayed initial migration phase to orientate towards the exit of the Baltic Sea.

## INTRODUCTION

The recognition of the dramatic downward trend in the European eel *Anguilla anguilla* (Linnaeus 1758) recruitment since the 1980s has led to numerous attempts to drive the stock recovery forward all over Europe (ICES, 2011a). Recovery measures differ between member states of the European Union, but are united under the aim of implementing the Council Regulation (EC) No 1100/2007 for the recovery of the *A. anguilla* stock. In order to reach the targeted 40% spawner escapement, relative to the best possible estimate of spawner biomass in a pristine state, the German Eel Management Plan (EMP) strongly relies on an extension of the nationwide stocking program (Anonymous 2008; ICES 2009a). In 2007, stocking in Germany accumulated to a total of approximately 10.1 million eels of different age and length classes (Anonymous 2008). To date, artificial reproduction of *A. anguilla* is still not feasible and stocking is dependent on (on-grown) glass eels and juveniles from the wild (Palstra et al. 2005). The European glass eel fishery is concentrated at the Atlantic coast around France and Spain with about 87% of European glass eel caught in the Bay of Biscay (Dekker 2000, 2003b). Therefore, stocking *A. anguilla* especially in northern European freshwaters generally implies extensive translocation of juveniles and could thus interfere with the possible imprinting of migration routes. So far, it has not been possible to ascertain the migration success of formerly stocked *A. anguilla* in the Baltic Sea beyond doubt, or the underlying mechanisms of orientation (Westin 1990, 1998, 2003).

Apart from securing the silver eel escapement from inland waters, the successful marine migration of silver eels to their spawning grounds in the Sargasso Sea is of equal importance to secure stock recovery. To date, the orientation mechanisms of eels on their spawning migration remain unclear. Nishi *et al.* (2004) demonstrated that Japanese eels *Anguilla japonica* (Timminck & Schlegel 1847) are magnetosensitive and proposed the geomagnetic field as a landmark for long-distance migration in eels. The same mechanism has subsequently been suggested by van Ginneken *et al.* (2005b) for the European eel. Other authors highlight the importance of olfaction rather than magnetic senses (Westin 1990). In general, diadromous fish are assumed to imprint their migration routes as juveniles and are thus able to find their way back to the spawning/natal sites (Hansen et al. 1993; Dittman and Quinn 1996). It has been proven that in anadromous fish even small scale translocations may impair adult homing behavior (Keefer et al. 2008). While in some cases yellow eels seem to be able to exhibit homing behavior after being relocated (Tesch 1970), very little is known about how large-scale translocations of glass eels might affect their migratory success as silver eels.

In previous investigations on the migratory behavior of stocked eels in the Baltic Sea, authors did not specifically consider eventual stocking histories of tracked individuals (Tesch et al. 1990;

Westin 1998; Limburg et al. 2003; Westin 2003; Westerberg et al. 2007). However, to appropriately investigate whether the translocation of eels has an impact on their spawning migration it is of major importance to elucidate individual life histories, including the origin of stocked eels. Glass eels for restocking are primarily caught in coastal waters and at the time of restocking have experienced only short periods in brackish waters (Dekker 2003b). Yet, over the past 20 years, the direct restocking of glass eels has decreased and has been compensated by an increasing use of elvers (bootlace eels) and yellow eels (ICES, 2010). Due to a temporal mismatch of glass eel arrival in the Bay of Biscay and stocking activities in northern Europe as well as the wide-spread belief that on-grown juveniles have a better chance of survival, the majority of glass eels dedicated for restocking are on-grown in aquaculture facilities prior to being released to the wild. Alternatively, but to a presumably minor extent, juvenile eels are being caught in freshwaters across Europe as restocking material.

In several recent investigations individual migration histories in a variety of diadromous fish species, including the European eel, could be successfully reconstructed by otolith microchemistry (Campana 2005; Arai et al. 2006; Hedger et al. 2008; Secor 2010; Marohn et al. submitted), whereby the strontium to calcium (Sr:Ca) ratio within the otolith served as a proxy for the surrounding water salinity (Campana 1999). To the authors' knowledge the present study is the first to combine a mark-recapture experiment of eels with otolith microchemistry analyses and thereby gathering information not only on possible migration routes after mark and release, but also on the importance of juvenile imprinting on the migration behavior of silver eels in the Baltic Sea.

Potential threats of restocking programs also include the introduction of alien species. Hence, the regular occurrence of *Anguilla rostrata* (Lesueur 1817) in German freshwater systems (Frankowski et al. 2009) is most likely due to illegal imports and trade of American glass eels or elvers for stocking purposes. Since *A. rostrata* and *A. anguilla* can hardly be distinguished by phenotypic traits (Boëtius 1980; Frankowski et al. 2009), it is necessary to preclude *A. rostrata* through genetic species identification to avoid possible misinterpretation of migration route/success of stocked eels due to unintentional tracking of anthropogenically introduced American silver eels. Maturing American eels, stocked to European freshwaters, would have experienced a translocation of a totally different magnitude and thus might bias the results.

The study objective was to determine whether stocked eels that had not been able to imprint on the migration route through the Baltic Sea due to translocation as juveniles are nevertheless equally capable of target-oriented migratory behavior towards the outlet of the Baltic Sea and to therefore ultimately assess the overall benefit of mass-translocation of juvenile *A. anguilla*.



## MATERIAL AND METHODS

### STUDY AREA

The Schwentine River system is located in northern Germany (Fig. 1). It has a total surface water area of approximately 7000 ha and consists of a series of freshwater lakes (approximately 5984 ha) that are connected by the Schwentine River. The system discharges into the Kiel Fjord (54°19'39"N 10°11'11"E) with an approximate average discharge of 3.9 m<sup>3</sup> s<sup>-1</sup>, ranging from 0.6 m<sup>3</sup> s<sup>-1</sup> to 13.4 m<sup>3</sup> s<sup>-1</sup>. It has been closed for ascending eels and other migrating fish species since 1904 by two consecutive hydropower stations (Figure III-1). No natural ascent of juvenile eels has been possible ever since and all eels in the system must have been stocked at some point either as glass eels, aquaculture grown or wild-caught elvers and yellow eels.

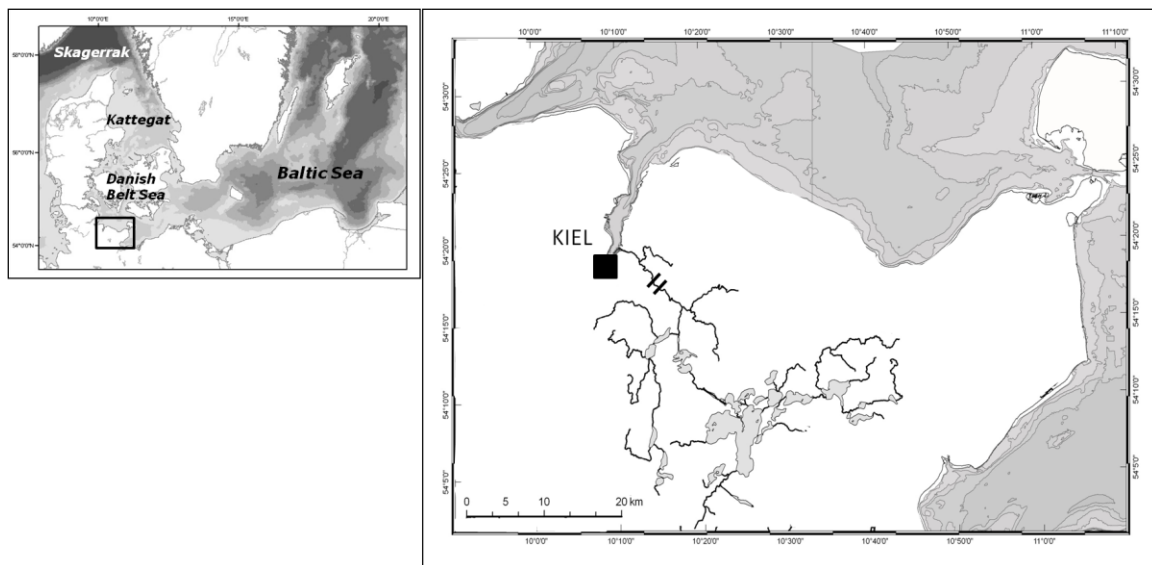


FIGURE III-1 Location of the Schwentine River system in northern Germany. The rectangle in the overview corresponds to the area of the main map. Black bars indicate the location of two hydropower stations. Additional rivers are not depicted.

### FISH TAGGING AND ANALYSIS AFTER RECAPTURE

All eels used in the tagging program were caught between September 2009 and April 2011 in a trap integrated in a fish pass at a hydropower station approximately 9 km upstream of the river mouth (Fig. 1). While the fish trap was active throughout the year, tagging concentrated on two “tagging periods” spring (March - June) and autumn (September - November) (Figure III-2).

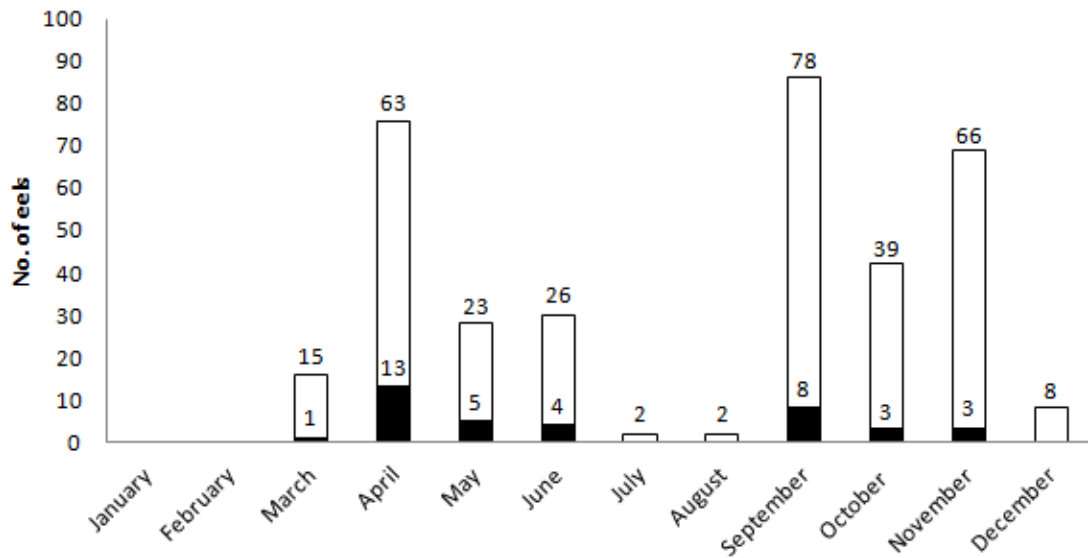


FIGURE III-2 Number of tagged [white bars] and recaptured *Anguilla* spp. [black bars] with corresponding tagging month

A total of 274 descending eels were individually tagged with yellow T-Bar anchor tags (Hallprint Pty Ltd.; Australia; <http://www.hallprint.com/>). Mean total length ( $\pm$  SD) of all eels tagged was  $79.5 \pm 9.1$  cm ranging from 45.7 to 104.7 cm and mean mass ( $\pm$  SD) was  $966.5 \pm 313$  g, ranging from 185 to 1975 g. The yellow marker on the tag had a size of 30 mm and carried contact information as well as an individual code. To increase tag reporting rate and to account for possible tag losses all eels were double-tagged (Björnsson et al. 2011). Tags were pinned in the epaxonic tail muscle clearly caudal of the anus using the dedicated tagging applicator supplied by Hallprint Pty Ltd. To reduce the risk of infections the tagging needle was disinfected (96% ethanol) and rinsed with sodium chloride solution (0.09%) prior to every single use. Tagging procedure lasted less than 15 sec per fish. Prior to the tagging, eels were weighed and photographed for subsequent length measurements to avoid using anesthetics and thereby minimize handling time and air exposure. Total handling time was kept to less than 2 min per fish. Total lengths were measured using Image Tool 3.0 (developed by the University of Texas Health Science Center, San Antonio; UTHACSA; <http://compdent.uthscsa.edu/dig/itdesc.html>) calibrated according to a scale depicted in each photo. A similar procedure has previously been tested on *Thunnus alalunga* (Bonnaterre 1788) with an accuracy of approximately 2.1% (Chang et al. 2010). Tagged eels were checked for onset of sexual maturation based on external features and assigned to one of the 5 different stages of migratory motivation introduced by Durif *et al.* (2005). Stages FIV and FV were considered to be real migrants (Durif et al. 2005). After the tagging procedure eels were transported downstream the hydropower stations and immediately

released into the Schwentine River (about 8 km upstream the river mouth) in order to allow an unobstructed, self-paced migration into the Baltic Sea.

Commercial and recreational fishermen were rewarded for reporting recapture date and position and returned tag and eel. When possible, time at liberty was calculated and net distance travelled was measured. In several cases, however, it was not possible to specify the exact time and/or location of recapture. Recaptured eels were collected and stored frozen (-40°C). After defrosting, biometric features, condition (as total fat content), otolith microchemistry and species identity were assessed. When possible, condition was checked as total fat content after Smedes (1999). For this, approximately 50 g (including skin) of filet from both body sides of the eel anterior to the anus was grinded into a homogenate. Total lipids were extracted from a known amount of homogenate with a solution of 2-propanol in cyclohexane. Total fat was expressed as per cent total fat mass per wet tissue. Freezing was considered to not influence fat content measurements (Ramalhosa et al. 2012). For detailed description of lipid-analysis see Karl *et al.* (2012).

#### OTOLITH PROCESSING AND MICROCHEMICAL ANALYSIS

The strontium/calcium (Sr:Ca) ratios in otoliths from recaptured eels were analyzed to confirm their individual migratory history. Sagittal otoliths were extracted and stored dry in Eppendorf caps. They were embedded in crystalbond Type 509 (Kager; Dietzenbach, Germany) and polished from the proximal side using lapping film (30, 12 and 3 MIC (3M; Neuss Germany)) until the core was exposed. Otolith Sr:Ca ratios were analyzed along the anterior-posterior growth axes by laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) using a UP193 solid-state laser (New Wave Research; Fremont, USA) coupled to a Finnigan Element 2TM (Thermo; Waltham, USA).

Instrumental settings were chosen as follows: Spot size: 75 µm; scan speed 3 µms<sup>-1</sup>; irradiance: ca. 1 GWcm<sup>-2</sup>; pulse rate: 10 Hz. As sample gas Helium was used (0.4 Lmin<sup>-1</sup>) and Argon was subsequently added (0.8 Lmin<sup>-1</sup>). Prior to every measurement transect surfaces were cleaned by preablation (spot size: 100 µm; scan speed: 100 µms<sup>-1</sup>). To account for possible instrumental drift a reference glass material (NIST612) was analyzed as external standard following every second measurement (concentrations are given in Pearce *et al.*, (1997). To assess data quality a pressed pellet of NIES22 otolith powder was repeatedly analyzed (National Institute for Environmental Studies; (Yoshinaga et al. 2000)).

Otolith Sr:Ca ratios were used to determine the time period individual eels spent in brackish or marine waters between metamorphosis and restocking. Values below 2.5 x 10<sup>-3</sup> were assumed

to indicate freshwater conditions (Daverat et al. 2006; Shiao et al. 2006). Freezing was assumed to not influence the measurements of Sr:Ca in the otoliths (Milton and Chenery 1998; Proctor and Thresher 1998).

Based on microchemistry, recaptured eels were assigned to one of two stocking-histories “pure freshwater” (F) and “brackish water experience” (BW). Individuals without a detectable brackish water signal were grouped as “freshwater” (Shiao et al. 2006). For those eels, previous Baltic Sea experience (prior to stocking) was ruled out. They were either stocked as glass eels, aquaculture grown elvers or as wild caught juveniles originating from a North Sea tributary. Individuals whose Sr:Ca profile showed a brackish water phase were assigned to “brackish water experience”. Even though, those eels must have been stocked into the Schwentine River as well, it is likely these eels had experienced the Baltic Sea environment prior to stocking and had been caught as stocking material in a Baltic Sea tributary.

#### SPECIES IDENTIFICATION

To reduce a potential bias by unintentional tagging of *A. rostrata* in the present study, all eels were genetically barcoded. When possible, white muscle tissue of recaptured eels was used to genetically screen for anthropogenically introduced American eel. Tissue samples were stored in 96% ethanol until analysis. Species identification largely followed the protocol of Frankowski and Bastrop (2010), based on mitochondrial cytochrome *b* and 18S rDNA restriction fragment length polymorphism (RFLP). However, due to supply shortage by the manufacturer the original protocol had to be adjusted by the use of different restriction enzymes. Instead of Baul and Paul (Frankowski and Bastrop 2010) BssS I and BssH II (New England Biolabs GmbH (NEB), Frankfurt/Main, Germany) were used for RFLP-analysis. Digestions lasted 4 h at 37°C (BssS) and 4 h at 50°C (BssH II). Resulting banding was visualized on a 1% agarose gel (incl. EtBr).

#### DATA ANALYSIS

Since freezing is known to reduce both length and mass, the measurements were corrected by 2.8% for mass and 2.5% for length (Wickström 1986). Fulton’s condition factor (*K*) was calculated as  $K = 100 * W/L^3$ , with *W* as body mass in g and *L* length in cm (Fulton 1904). For the statistical analysis, recaptured eels were assigned to one of two tagging periods (spring and autumn). “Net distance” traveled was measured as shortest possible route between release site and recapture location. Additionally, “coastal distance” was measured as possible migration route following the coastal line. “Time at liberty” was calculated using the release date and reported recapture date. When the day of recapture could not be determined with certainty (8 eels, 28%) but only the

calendar week was provided, the Wednesday of this week was taken as recapture date. “Rate of travel” was calculated as “net distance” [km] divided by “time at liberty” [days]. “Coastal rate of travel” was calculated as “coastal distance” [km] divided by “time at liberty” [days]. The influence of tagging period (“spring” and “autumn”) and individual life history (“freshwater” or “brackish water experience”) on “rate of travel”, “coastal rate of travel”, “net distance”, fat content and “time at liberty” was tested for significance by nonparametric Kolmogorov-Smirnov test. All correlations were checked for significance by Pearson  $r$ . Level of significance was set to be  $p = 0.05$ . All statistical tests were performed in STATISTICA 8.0 (StatSoft Inc.).

## RESULTS

Of the 274 tagged and released eels, 29 were reported recaptured corresponding to a recapture rate of approximately 11%. Most recaptured individuals were identified as actively migrating eels at time of tagging, with stage FIV accounting for 41% and FV for 28% (Table I). Six eels (~ 21%) were stage FII or FIII at time of tagging and have thus to be considered not yet migrating (Durif et al. 2005). However, it was possible to retrieve 4 out of those six eels (previously staged not yet migrating) for staging after recapture. All of them (Tag ID: 1214, 1241, 1228 and 1209) were stage FV after recapture (Table III-1). In addition, 3 eels (Tag ID: 1106, 1248 and 1303) staged FIV at time of tagging were stage FV after recapture (Table III-1). One eel (Tag ID: 0057) was stage FIV at time of tagging but FIII after recapture.

TABLE III-1 Summary of tagging group, individual life history prior to stocking, species affiliation and migratory behavior, when available. Tag ID corresponds to one of the two T-Bar Anchor Tags for each eel.

Tag ID	Tagging Group	Individual life history	Species	Silver Stage		Time at Liberty [days]	Net Distance [km]	Rate of Travel [km day <sup>-1</sup> ]	Coastal Rate of Travel [km day <sup>-1</sup> ]
				*	**				
1106	spring	F	<i>A.anguilla</i>	FIV	FV	154	12	0.1	0.1
1162	spring	-	-	FIV	-	149	94	0.6	1.0
1164	spring	-	-	FIV	-	155	30	0.2	0.2
1169	spring	BW	<i>A.rostrata</i>	FV	-	192	140	0.7	1.1
1178	spring	F	<i>A.anguilla</i>	FV	FV	42	5	0.1	0.1
1207	spring	-	-	FIII	-	133	74	0.6	0.6
1209	spring	BW	<i>A.anguilla</i>	FII	FV	154	75	0.5	0.9
1214	spring	BW	<i>A.anguilla</i>	FIII	FV	27	13	0.5	0.5
1228	spring	F	<i>A.anguilla</i>	FIII	FV	171	75	0.4	0.8
1239	spring	F	<i>A.anguilla</i>	FV	FIV	77	144	1.9	3.1
1241	spring	BW	<i>A.anguilla</i>	FIII	FV	185	140	0.8	1.2
1248	spring	F	<i>A.anguilla</i>	FIV	FV	85	12	0.1	0.2
1266	spring	-	-	FIV	-	135	310	2.3	3.0
1280	spring	-	-	-	-	117	144	1.2	2.0
1303	spring	BW	<i>A.anguilla</i>	FIV	FV	199	75	0.4	0.7
1307	spring	-	-	FIII	-	123	81	0.7	0.9
1344	spring	-	-	FIV	-	144	15	0.1	0.1
1612	spring	-	-	FIV	-	77	12	0.2	0.2
0003	autumn	BW	<i>A.anguilla</i>	FV	FV	68	144	2.1	3.6
0057	autumn	F	<i>A.anguilla</i>	FIV	FIII	66	75	1.1	2.1
0065	autumn	-	-	FIV	-	416	95	0.2	0.3
0088	autumn	-	-	FIV	-	363	70	0.2	0.2
1040	autumn	F	<i>A.anguilla</i>	FV	FV	310	75	0.2	0.5
1370	autumn	F	<i>A.anguilla</i>	FV	FV	33	110	3.3	5.2
1390	autumn	F	<i>A.anguilla</i>	FV	FV	48	75	1.6	2.9
1413	autumn	-	-	FIV	-	328	20	0.1	0.1
1519	autumn	F	<i>A.anguilla</i>	-	FV	59	75	1.3	2.4
1631	autumn	-	-	FIV	-	281	124	0.4	0.6
1699	autumn	-	-	FV	-	356	273	0.8	1.2
mean ( $\pm$ SD)						160( $\pm$ 108)	89.2( $\pm$ 72)	0.8( $\pm$ 0.8)	1.2( $\pm$ 0.03)

\* after Durif et al. (2005) at release

\*\* at recapture

life history : F = freshwater; BW = brackish water

Figure III-3 shows all reported recapture locations. In summary, one single eel (~ 3%) was reported from the Kattegat (i.e. in the connection between the Baltic Sea and the North Sea), one eel (~ 3%) from the Øresund (between Denmark and Sweden) and 16 eels (~ 55% of recaptures) were reported from the direction of the Danish Belt Sea, the connection between the Baltic Sea and the North Sea. In addition, 8 eels (~ 28%) were already caught within the Kiel Fjord region, with one caught still in the Schwentine River. Three eels (~ 10%) were caught around the German island of Fehmarn, about 80 km eastwards from the river mouth.

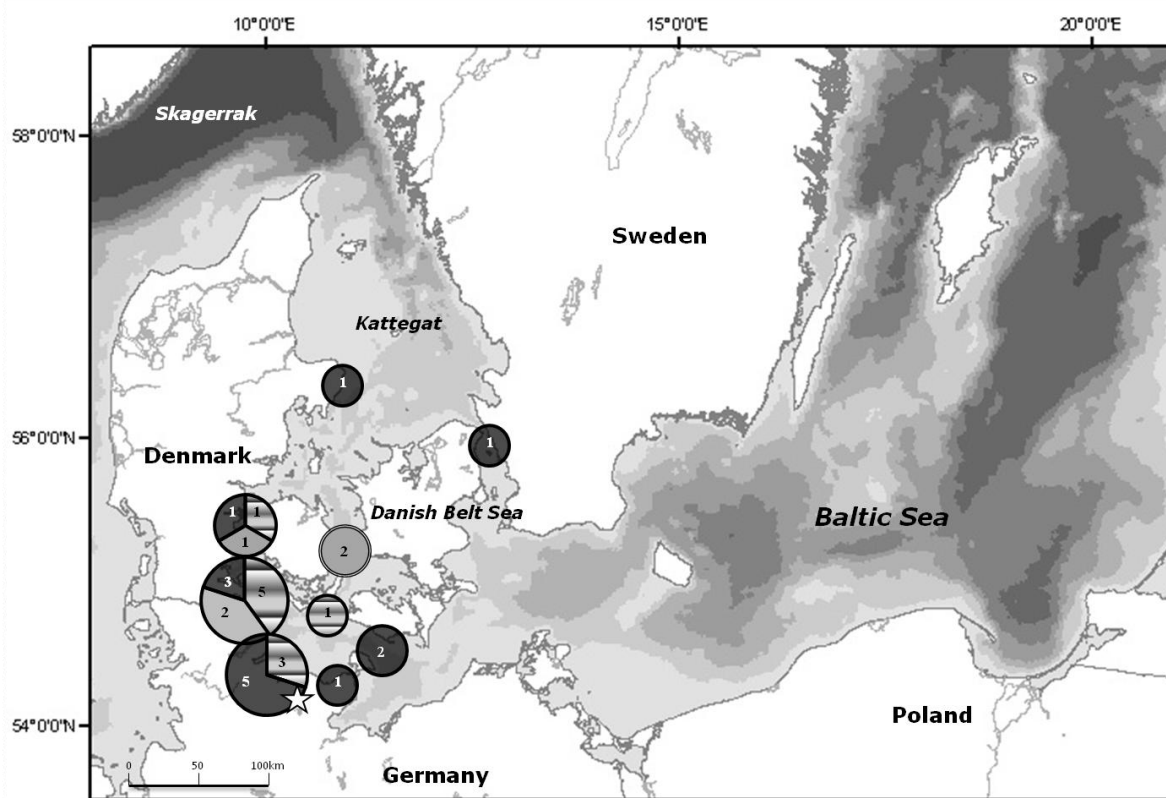


FIGURE III-3 Recapture locations and individual life histories of T-Bar tagged *Anguilla* spp. in the Baltic Sea. Circles represent areas with accumulated recaptures. Subdivisions of circles represent individual life histories. Crosshatched = freshwater; grey = brackish water experience; black = not available. Numbers are of individuals according to life histories. Location site highlighted by broken lining indicates the recapture site for the single *A. rostrata* individual. The release site is indicated by the white star.

Recaptured eels spent on average  $160 \pm 108$  days ( $\pm$  SD) at liberty. Shortest time to recapture was 27 days and longest time at liberty was 416 days (Table III-1). Mean “net distance” traveled until recapture was  $89 \pm 72$  km ( $\pm$  SD). Shortest “net distance” was approximately 5 km and longest “net distance” was approximately 310 km (Table III-1). Mean “coastal distance” traveled was  $138 \pm 108$  km ( $\pm$  SD). Recaptured eels ( $n = 29$ ) showed a mean “rate of travel” of  $0.8 \pm 0.8$  km ( $\pm$  SD) day<sup>-1</sup> towards the recapture locations ( $< 0.1 - 3.3$  km day<sup>-1</sup>; Table III-1). Mean “coastal rate of travel” was  $1.2 \pm 0.03$  km ( $\pm$  SD) km day<sup>-1</sup> ( $< 0.1 - 5.2$  km day<sup>-1</sup>, Table III-1). Eels released in spring ( $n = 18$ ) and those released in autumn ( $n = 11$ ) did not differ significantly in “rate of

travel”, “coastal rate of travel”, “net distance” or “coastal distance” (Kolmogorov-Smirnov test  $p > 0.1$ ). However, “time at liberty” was significantly shorter in eels released in spring (Kolmogorov-Smirnov test  $p < 0.05$ ).

Out of the 29 reported recaptures it was possible to retrieve 16 (~ 55%) eels for further analysis. When possible, otolith microchemistry (16 eels) was checked for Sr:Ca along a transect from the core to the outer edge of the otolith. Out of the 16 analyzed eels 10 (~ 62.5%) had an otolith Sr:Ca profile indicating no previous brackish water experience (F). Those profiles are characterized by high Sr:Ca ratios in the core region representing the larval phase followed by a sudden drop to values below  $2.5 \times 10^{-3}$  under freshwater conditions. The remaining six analyzed eels (~ 37.5%) had otolith Sr:Ca profiles that clearly showed a prolonged brackish water phase (BW) at some point in their life prior to restocking. Individual life history did not have a significant effect on any of the migration parameters (Kolmogorov-Smirnov test,  $p > 0.1$ ). Figure III-3 summarizes the different individual life histories and allocates them to recapture locations. No trend in recapture location dependent on individual life history was observed.

It was possible to determine the fat content of 12 retrieved eels. On average the total fat content after recapture was  $28.4\% \pm 4.4$  ( $\pm$  SD). Lowest total fat content documented was 22.6% and highest total fat content was 37.0%. All eels for which this analysis was possible lost in mass and all but one in length. Length and mass development of those 12 recaptured eels is shown in Table III-2. Additionally, Fulton’s condition factor ( $K$ ) decreased between release and recapture in all but two (Tag ID: 1214 and 1241) of the 12 eels. Average Fulton’s condition factor ( $K$ ) changed from  $0.19 \pm 0.03$  ( $\pm$  SD) at time of release to  $0.17 \pm 0.03$  ( $\pm$  SD) after recapture (Table III-2). There was neither a significant correlation between “total fat content” and “net distance traveled” (Pearson  $r = 0.05$ ,  $p = 0.86$ ) or “time at liberty” (Pearson  $r = -0.15$ ,  $p = 0.64$ ), nor between the decrease in Fulton’s  $K$  and “distance traveled” (Pearson  $r = 0.31$ ,  $p = 0.33$ ) or Fulton’s  $K$  and “time at liberty” (Pearson  $r = -0.02$ ,  $p = 0.95$ ).



**TABLE III-2**  $L_T$ , mass and condition factor of *Anguilla* spp. At release and changes at recapture (when available). Values at recapture were corrected for freezing.

Tag ID	at release		at recapture		at release	at recapture
	$L_T$ [cm]	Mass [g]	$\Delta L_T$ [cm]	$\Delta$ Mass [g]	Fulton's <i>K</i>	Fulton's <i>K</i>
0057	75.2	1007	-0.8	-156	0.24	0.21
1040	70.5	580	-1.9	-128	0.17	0.14
1106	84.5	1230	0.3	-54	0.20	0.19
1178	70.8	540	-2.0	-130	0.15	0.13
1209	72.4	620	-1.0	-147	0.16	0.13
1214	82.8	980	-2.2	-67	0.17	0.17
1228	81.5	865	-2.5	-144	0.16	0.15
1239	69.2	735	-2.1	-220	0.22	0.17
1241	73.2	685	-0.9	-31	0.17	0.17
1248	86.8	1430	-1.5	-163	0.22	0.20
1303	82.8	1036	-2.8	-146	0.18	0.17
1390	77.0	987	-0.2	-119	0.22	0.19
mean ( $\pm$ SD)	77.2	891.3	-1.5( $\pm$ 0.9)	-125.3( $\pm$ 50.1)	0.19( $\pm$ 0.03)	0.17( $\pm$ 0.03)

It was possible to analyze 16 of the recaptured eels for species identity of which one individual turned out to be *Anguilla rostrata* (Tag ID: 1169). The specimen was caught after approximately 190 days 140 km north of the release site, close to Nyborg off the Danish island of Fyn.

## DISCUSSION

So far, tagging experiments with *A. anguilla* in the Baltic Sea have primarily been performed on the east coast of Sweden with release sites off Gotland (Tesch et al. 1990; Westin 1998, 2003) and Öland (Westerberg et al. 2007). Recapture locations from all of these studies indicate a southwesterly migration before turning north at the most southern tip of Sweden. In contrast, eels released in the present study had to choose a northward direction right after release to reach the North Sea and successfully continue their migration. Recapture rate in the present study is in line with previous investigations. Westin reported recapture rates between 7.8% (1990) and around 15% (1998) for stocked *A. anguilla* and up to 35% for wild *A. anguilla* (1998). He showed that recapture rates for stocked *A. anguilla* are often lower than for naturally recruited *A. anguilla* and suggested that fewer recaptures are likely a result of delayed migration of stocked eels and therefore of lower catchability by commercial and recreational fishers. This might hold true in the present study.

In the present study, total recapture through commercial and recreational fisheries might be biased by non-reported catches, since in light of the ongoing discussion about European eel

management, the motivation to support scientific studies is considered to be low. In addition, the predominance of recapture reports from Denmark could be a result of the intensive and targeted silver eel fishery in Danish marine waters. However, since coastal marine (eel) fisheries exist in all countries bordering the Baltic Sea (ICES 2010a, b), the systematic error based on differences in fishing effort was considered to not significantly affect the results.

Of the reported 29 recaptures, 13 (~ 45%) were caught in the straight between the Danish island of Fyn and the Jutland Peninsula (the Little Belt), straight north of the release site in direction of the Baltic Sea outlet. Additionally, three eels were caught in the Great Belt again indicating a clear northward orientation. However, “rate of travel” in the present study might suggest difficulties in orientation towards the exit of the Baltic Sea compared to Westerberg *et al.* (2007), who reported mean rates of travel for eels in the Baltic Sea to be a multiple (10 to 20 km d<sup>-1</sup>) of the present findings.

In the present study the eels were released back into the Schwentine River about 8 km from the outlet. Eels delaying their downstream migration after the tagging procedure could therefore lead to an underestimation of the actual “rate of travel”. Nevertheless, as most of the recaptured eels were identified as active migrants at time of catch and release, prolonged stopovers in the river are not likely. Breukelaar *et al.* (2009) documented average migration speeds of downstream migrating silver and yellow eels in the River Rhine of 0.34 m s<sup>-1</sup> (approximately 30 km d<sup>-1</sup>), about 10 times higher than average overall migration speed found in the present study with particularly low migratory activity between January and August. However, for eels released in spring (March to June) that might have waited for the autumn silver eel run and stayed longer in the Schwentine River before starting their migration, the average “rate of travel” should have been significantly lower than of those eels released in autumn. This did not hold true in the present results.

It has to be considered that eels instead of choosing/finding the shortest way to the outlet of the Baltic Sea rather migrate close to shore (Westerberg *et al.* 2007). This would multiply the actual distance covered from release site to recapture location. However, the “rate of travel” corrected for “coastal distance” was still about one magnitude lower than given by Westerberg *et al.* (2007). Davidsen *et al.* (2011) documented an average migration speed of 0.5 km d<sup>-1</sup> for eels released in an acoustic tracking study in a Norwegian fjord. They suggested that the low migration speed (with large individual variations) might be due to different small-scale current speeds or directions at sea entry. This might hold true for the present study as well. Silver eels searching for the route out of the Baltic Sea close to shore would encounter several small-scale

current systems that influence individual migratory behavior and result in the documented “rate of travel”.

With 62.5% of the analyzed eels showing an otolith Sr:Ca profile that excludes any previous prolonged brackish water experience, the common practice of stocking *A. anguilla* that had never experienced the Baltic Sea before could be analytically confirmed. The remaining 37.5% were likely stocked as yellow eels and it was not possible to exclude previous Baltic Sea experience. In addition, possible misinterpretation of migration route/success of stocked eels due to unintentional tracking of anthropogenically introduced *A. rostrata* was precluded through genetic species identification.

Migratory motivation has been described to be triggered predominantly by sufficient fat/energy reserves (Larsson et al. 1990). Svedäng and Wickström (1997) showed that silver eels in the Baltic Sea originating from freshwater systems often have an insufficient muscle fat content. They suggested that as a result stocked eels prolong their initial migration phase in coastal waters for feeding and replenishing their energy storage. Limburg *et al.* (2003) pointed out that eels exiting the Baltic Sea had higher fat contents than those collected inside the Baltic and equally suggested a potential fill up of fat storages. In the present study, even the lowest total fat content measured after recapture (22.6%) exceeded the minimum requirement for a successful migration given by Van den Thillart *et al.* (2007). However, length and mass development strongly contradict these suggestions as all eels lost mass between release and recapture. Ongoing feeding in the Baltic Sea leading to an increase of energy storage should have prevented loss of mass and counteracted the documented decrease in Fulton’s condition factor (*K*) during migration. The idea of prolonging the initial migratory phase to fill up energy storage can therefore be rejected for eels in the present study.

The documented “rate of travel” suggests that formerly stocked European silver eels may have difficulties finding the exit of the Baltic Sea independent of their individual life history prior to stocking. Nevertheless, recapture locations indicate the general capability of eels to eventually find the exit of the Baltic Sea. Even the single eel identified as *Anguilla rostrata* did not differ in its migratory behavior from the *A. anguilla* and was able to somehow locate the exit. Therefore, orientation mechanisms seem to be independent of previous migration-experiences as immigrating juveniles. Present findings further support the idea of Tesch (1974), who suggested a combination of geomagnetism and salinity being the orientation-driving mechanism. Without the possibility to imprint the migration route, the search for higher salinity water bodies and orientation in the geomagnetic field could explain the delayed orientation towards the Kattegat.

In summary, documented behavior might be interpreted as a delay during the initial migration phase to orientate towards the exit of the Baltic Sea. Despite the limited number of case-studies, the “rate of travel” of silver eels in the Baltic Sea documented here is considered to be extremely low. It has to be questioned whether stocked eels migrating across the Baltic Sea are capable of successfully participating in the spawning event in the Sargasso Sea, as that would not only require homing to the natal site but also being able to arrive in time for the following spawning event in early spring (Tesch 2003). One of the few studies on presumably stocked European eels in the Baltic Sea came to a similar conclusion (Westin 1998). A delayed initial migration phase of stocked eels inside the Baltic Sea and the related potential loss of silver eels from the effective population size have to be considered when assessing management measures for the recovery of the *A.anguilla* stock.

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## CONCLUSIONS

The results summarized in this thesis do not defuse the dramatic situation of the European eel stock but actually highlight the urgent need to rethink the present eel management policy. As part of the data accumulation for the Eel Management Plans all over Europe, the devastating stock situation was not only confirmed but often identified to be even more severe. At the same time, already applied management measures, if ever, are not expected to show measurable effects for the next 10-20 years (Anonymous 2012). Unfortunately, the still far-reaching uncertainties about the biology of *A. anguilla* and the split between species-conservation and commercial interests complicate a sound and sustainable recovery of the European eel stock (Feunteun 2002).

The exceptional life-cycle of the European eel challenges management authorities and requires a European approach (Feunteun 2002). The European eel stock is considered to be out of safe biological limits (Dekker 2003b; ICES 2011a) and the presumably panmictic population structure with a single spawning area increases the chance of a population-wide reproductive failure due to depensation (Liermann and Hilborn 1997; Dekker 2003a; Russell and Potter 2003) and to oceanic changes that inhibit the successful recruitment of glass eels to continental waters (Friedland et al. 2007; Bonhommeau et al. 2008a). A complete recruitment failure would exacerbate the current situation and easily boycott European eel management plans as they are largely based on the translocation of juveniles to support stocking programs all over the distribution area (Feunteun 2002; ICES 2011a).

The EU Council Regulation No. 1100/2007 (“Eel Regulation”) might therefore constitute a good basis for the stock recovery by setting a minimal limit of silver eel escapement from European inland waters (European Union 2007). The 40% escapement goal (with respect to a pristine state), however, is rather arbitrary and without any scientific basis its usefulness for the stock recovery will remain speculative. Up to date, it remains unclear whether the decrease of the European eel stock is primarily driven by (anthropogenic) continental factors or rather the result of oceanic changes. In case the stock decline is primarily based on the lack of recruitment due to changes in the North Atlantic ocean conditions (Friedland et al. 2007) and/or poor food availability on the natal side (Knights 2003; Bonhommeau et al. 2008b), an increase of the spawner escapement may not sustainably support the stocks’ recovery and the 40% escapement goal would have to be considered ineffective. Only when the successful recruitment to

continental waters is guaranteed, an increase of escapement could actually help impel the stock recovery. In any case, while it remains to be scientifically proven whether the 40% escapement goal is actually sufficient to sustainably increase the stock size, it is one of the few management measures affecting the amount of spawners immediately.

Regardless of the uncertainties escorting the general idea of a fixed escapement goal, the results presented here document the problems with its implementation. In the absence of a complete documentation of former and actual spawner escapement numbers, management authorities are forced to evaluate the success of management measures on “best estimates”. Trans-regional estimations of escapement numbers are, however, inevitably biased by generalization and resulting incorrect estimations may highly influence both the evaluation of the current stock situation and future management decisions.

In **Chapter I** we were able to highlight the importance to carefully reconsider the estimates of  $B_{\text{current}}$  used so far and to improve the methodology to assess the actual escapement of silver eels. Missing the 40% escapement target might be alarming. The discrepancy between the real spawner escapement from a single river system documented here and estimated  $B_{\text{current}}$  for the respective eel river basin as documented in **Chapter I** on the other side, illustrates a problem potentially boycotting the efforts to stop the downward trend of the European eel stock. The uncertainties of silver eel escapement estimates may lead to severe misinterpretations of the actual spawner output. While spawner escapement for the eel river basin “Schlei/Trave” had to be estimated based on the available time series, we were able to directly document the silver eel escapement from the Schwentine River system (**Chapter I**). A likewise comprehensive assessment of escaping silver eels is, however, rarely possible (especially on an eel river basin level). The application of population dynamic models to estimate the spawner production and escapement is therefore inevitable and several authors have published model approaches to describe eel stock dynamics (Arahamian et al. 2007; Bevacqua et al. 2007; Amilhat et al. 2008). It is strictly necessary to evaluate how close to reality the used population dynamics models are. To test the performance of the widely used German Eel Model, we cumulated the required input data and compared the model results for the Schwentine River system with the actually documented silver eel escapement (**Chapter II**). Results seem to document the potential of the GEM II as useful tool when estimating the potential silver eel output of inland waters with modeled escapement closely resembling the actually documented silver eel output. At the same time, however, **Chapter II** delineates the importance of a time- and effort-consuming monitoring

to assess the necessary system-specific input parameter. Unfortunately, it is hardly feasible to establish a distribution-wide complete assessment of input data needed for a likewise estimation of  $B_{\text{current}}$ , because both of logistical reasons and geographical features of the individual eel river basins. The provision of the most realistic modeled estimate of escapement numbers will, however, only be possible by minimizing the number general assumptions used and including system-specific population characteristics. It is, therefore, highly important to adjust current sampling strategies to provide the necessary system-specific characteristics of local eel populations and allow a sound modeling of escapement numbers.

Even though it is not explicitly stated in the EU Eel Regulation, its measures are primarily restricted to the freshwater phase of *A. anguilla* (European Union 2007). Nevertheless, recent studies have shown that substantial numbers of eels are never entering the continental freshwaters and rather spend their entire life in coastal marine and brackish habitats. A quantitative assessment of these coastal residents is, up to date, still lacking and their numbers can hardly be included in European stock estimates. Including coastal residents in the management measures would ultimately increase the efficiency of overall stock protection.

Silver eels managing to survive the numerous threats in inland waters and escape from freshwaters all over Europe are only at the beginning of an ambitious migration towards the spawning ground. Béguer-Pon et al. (2012) suggested that sharks might represent a significant source of mortality for silver stage American eels during their early marine migration and European eels entering the marine habitats might be equally threatened by large predators. Therefore, silver eels leaving inland waters would be expected to show fast and target-oriented migratory behavior towards the deeper ocean to rapidly leave the shelf areas and thereby avoid (e.g.) predation. Migration speeds of tracked individuals in **Chapter III**, however, indicate that such a target-oriented migration can be significantly slowed down, possibly effected by lack of imprinting. Our results show that the transfer of juvenile eels to northern European inland waters could possibly disturb their ability to locate the shortest migration route leading to a delayed initial migration phase. This delay by itself may cause silver eels that eventually find the exit into the North Sea and proceed with their migration towards the spawning ground, to miss the actual spawning event. In addition, a prolonged stay in coastal marine/brackish waters would not only increase the risk of predation by (e.g.) large cod (*Gadus morhua*) or ling (*Mova mova*), but also the chance of being caught in coastal fisheries virtually present all along the Baltic coast line. While the density of predators big enough to prey on female silver eels is

probably rather low in the Baltic Sea, coastal eel fishery poses a real threat to migrating eels. Previous studies have shown that migrating silver eels are especially vulnerable to coastal fisheries as they are migrating close to shore (Westin 1998; Westerberg et al. 2007). In any case, silver eels migrating out of the Baltic Sea will eventually have to pass the Danish Belt Sea. The three possible migration pass ways between the Danish islands constitute a bottleneck that every single eel migrating out of the Baltic Sea has to pass (for the case that the Kiel Canal is not considered to be an actual route of choice) with eel fisheries being present in all of them. Most of the recaptures in **Chapter III** were reported from the Small Belt documenting the high impact of (coastal) eel fisheries on migrating silver eels in the Baltic Sea.

Much has been discussed about the contribution of silver eels originating from stocking to the effective population size of *A. anguilla*. The here presented results highlight the importance to rethink the restriction of the European eel management to inland waters and the current policy to stock northern European waters with glass eels from the Atlantic coast. As mentioned above, the prolonged early marine migration due to the lack of imprinting increases the risk of silver eels being lost by predation or fishery. Specific geographic features of the Baltic Sea (migration bottleneck in the Danish Belt Sea), in particular, require the extension of current eel management to marine (or brackish) waters. It is, therefore, highly desirable to support the idea of creating a large-scale management unit "Baltic Sea". Its effectiveness would, however, again rely on a sound assessment of the silver eel output of all freshwater systems entering the Baltic Sea to assess the potential overall silver eel output of the Baltic Sea region.

To summarize, virtually every life stage of the European eel is threatened by often multiple factors, reducing both the overall silver eel escapement and the reproductive potential of individuals and numerous authors have identified various factors contributing to the downward trend of the European eel stock (Dekker 2003a; Friedland et al. 2007; Bonhommeau et al. 2008b; Calles et al. 2010; Henderson et al. 2012). The hierarchy of mortality factors is, however, still subject of controversy and it has become obvious that it will hardly be possible (and maybe not even reasonable) to identify one single factor being solely responsible for the decline (Wysujack 2007). All the more, it is necessary to consider the precautionary approach defined by the FAO (1995) in the "*Code of conduct for responsible fisheries*" and reduce the overall mortality as much as possible. Minimizing all anthropogenic mortalities and influences would eventually mean to reduce or cease stocking. For a lot of freshwater systems all over Europe this would ultimately result in the absolute absence of recruitment (at least as long as the natural



recruitment does not improve) and thus likely to the demise of artificially sustained eel populations. The summarized results presented here, however, strongly question the usefulness of artificially sustaining an eel population in systems that only yield a limited amount of silver eels for the overall recovery of the *A. anguilla* stock.

Effective species conservation requires the best possible characterization of reasons for the decline. Only then will it be possible to adjust the management decision in order to impel the stock recovery. The lack of knowledge must, however, not be used as an excuse for postponing far-reaching stock enhancement measures to save the European eel from extinction.

## **OUTLOOK AND FUTURE CHALLENGES IN EEL MANAGEMENT**

Despite the intense research, essential basics of the biology of *A. anguilla* are still only inadequately known. Above all, natural mortality is still subject of a European-wide discussion. As management measures often have to be based on model assumptions, natural mortality is, however, often a critical parameter necessary for a sound model of the population dynamics. It is, therefore, highly desirable to substantiate the current understanding of natural mortality in *A. anguilla* with subsequent *in situ* investigations.

Additionally, it is necessary to further disentangle the complex interactions of the numerous mortality factors for eels in European inland waters. Hereby, the aim should not be to identify one single reason for the stock decline, but rather to further pinpoint possible support for a fast and sustainable recovery. Even though the present thesis constitutes a good starting point for such analysis, its restriction to a medium-sized freshwater system limits the transferability onto nation-wide stock dynamics. Future focus should, therefore, be directed to larger freshwater systems. This has, obviously, been done during both the assessment and the implementation of the Eel Management Plans. During this process, however, it became obvious that a sound assessment requires a much more detailed documentation of the system-specific population characteristics. It will thus be necessary to improve the current assessment of (e.g.) spawner numbers to prevent the misinterpretation of the potential silver eel output of a specific catchment.

Results presented here clearly show the urgent need to further clarify the impact of large-scale translocation of juvenile eels on their capability to successfully participate in the spawning event. Even though our results question the usefulness of distributing juveniles caught at the Atlantic coast all over Europe, additional studies are needed to allow for a concluding advice. In addition, the fate of silver eels (stocked and natural recruited) during their long-distance migration to the spawning ground needs to be further disentangled. The recent technological progress has led to a significant reduction in the size of satellite tags and their application might unveil some of the remaining mysteries.

Finally, as long as it is not possible to artificially reproduce the European eel on a commercial scale, extenuating the stocks' decrease and supporting its recovery will eventually depend on the reduction of anthropogenic pressure on the natural population. Therefore, it will be

essential to close the still present gaps in the species' biology and facilitate the artificial reproduction. This would support the establishment of brood-stocks and at the same time would solve the ubiquitous dilemma of commercial interests versus species conservation.

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## List of Publications

All chapters of the present thesis were prepared to be submitted to peer-reviewed scientific journals. At the time of submitting this thesis, all chapters were already submitted and in the review process. Submitted manuscripts were adjusted to journal-specific formatting.

### Chapter I

Marohn, L., **Prigge, E.**, Hanel, R. A long way down – escapement success of silver eels from a German river system. *Freshwater Biology* (under review)

### Chapter II

**Prigge, E.**, Marohn, L., Oeberst, R., Hanel, R. (2013) Model Prediction versus Reality – Testing the predictions of a European eel (*Anguilla anguilla*) stock dynamics model against the *in situ* observation of silver eel escapement in compliance with the European Eel Regulation. *ICES Journal of Marine Science*, DOI:10.1093/icesjms/fss188

### Chapter III

**Prigge, E.**, Marohn, L., Hanel, R. (2013) Tracking the migratory success of stocked European eels (*Anguilla anguilla*) in the Baltic Sea. *Journal of Fish Biology* 82 (2), p. 686-699, DOI:10.1111/jfb.12032

In addition, following manuscripts (that are not part of this thesis) were published between 2009 and 2012:

**Prigge, E.**, Mahl Zahn, A., Zumholz K., Hanel, R. (2012). Dietary effects on fatty acid composition in muscle tissue of juvenile European eel, *Anguilla anguilla* (L.). *Helgoland Marine Research* 66 (1), p 51-61, DOI: 10.1007/s10152-011-0246-3

**Marohn, L., Prigge, E.**, Zumholz, K., Hanel, R. (2009). Dietary effects on multi-element composition of European eel (*Anguilla anguilla*) otoliths. *Marine Biology* 156 (5), p. 927-933, DOI: 10.1007/s00227-009-1138-9

## **Contributions of the Authors**

All chapters of this thesis were designed to be published in peer-reviewed journals. The following list clarifies my personal contribution to each manuscript.

### **Chapter I - Silver eel escapement and quality in an exemplary German river system**

The investigation was designed by Reinhold Hanel, Lasse Marohn and Enno Prigge. Silver eel monitoring at the fish pass, parasitological examination, age-reading and third-party data (fisheries, environmental factors) collection were done by Lasse Marohn and Enno Prigge. Catch and stocking data was analyzed by Lasse Marohn and Enno Prigge. Analysis of environmental factors was done by Lasse Marohn. Acoustic telemetry tagging and analysis of results were done by Enno Prigge and Lasse Marohn. Fat analysis was done by Enno Prigge. The manuscript (including all graphics) was written by Lasse Marohn and improved by all co-authors.

### **Chapter II - Model Prediction versus Reality – Testing the predictions of a European eel (*Anguilla anguilla*) stock dynamics model against the *in situ* observation of silver eel escapement in compliance with the European Eel Regulation**

The study was designed by Enno Prigge, Lasse Marohn and Reinhold Hanel. Data collection was done by Enno Prigge and Lasse Marohn. Model adjustments were performed by Enno Prigge and Rainer Oeberst. Parameter fitting was done by Enno Prigge. The manuscript (including all graphics) was written by Enno Prigge and improved by all co-authors.

### **Chapter III - Tracking the migratory success of stocked European eels (*Anguilla anguilla*) in the Baltic Sea**

The study was designed by Enno Prigge, Lasse Marohn and Reinhold Hanel. T-bar tagging was performed by Enno Prigge. Microchemistry of the otoliths was analyzed by Lasse Marohn. Recapture data was analyzed by Enno Prigge. The manuscript (including all graphics) was written by Enno Prigge and improved by all co-authors.



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HERZLICHEN DANK

## CURRICULUM VITAE

### PERSONAL DETAILS:

Name & Surname: Enno Prigge  
Date of Birth: 04 July 1981  
Place of Birth: Hannover (Germany)  
Nationality: German

### EDUCATION:

Sep 2008 – Nov 2012: Elaboration of PhD-thesis at the the Helmholtz-Centre for Ocean Research (GEOMAR)  
Thesis title: “Factors challenging the European eel (*Anguilla anguilla*) stock recovery in continental waters”

14<sup>th</sup> of May 2008: Diploma Degree, Thesis title: “The influence of diet on fatty acid and stable isotope composition in European eel (*Anguilla anguilla*)”

Feb 2006 – Aug 2006: Studies abroad at the Syddansk Universitet, Odense

Oct 2005 – Aug 2006: Participant of the International Study Program “Biological Oceanography”

2001 to 2008: Student (Biology, Diplom) at the Christian Albrechts University, Kiel  
Area of Specialisation: “Biological Oceanography”  
Subsidiary Subjects: “Zoology” and “Ecosystem Theories”

27 June 2000: School leaving examinations (Abitur) at the Ricarda-Huch-Schule, Hannover, Germany  
Exam Subjects: Biology, Mathematics, Geography, German

**WORK EXPERIENCE:**

- July 2012 – present: Scientist at the Helmholtz-Centre for Ocean Research (GEOMAR), Kiel (until 2012: Institute of Marine Science, IFM-GEOMAR). Research division: FB3, Marine Ecology / Evolutionary Ecology of Marine Fishes
- Sept 2008 – July 2012: Scientist at the Helmholtz-Centre for Ocean Research (GEOMAR), Kiel (until 2012: Institute of Marine Science, IFM-GEOMAR) Research division: FB3, Marine Ecology / Evolutionary Ecology of Marine Fishes  
Project: “Quantification of Mortalities for the European eels (*Anguilla anguilla*) in German inland waters”, Funded by the “Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz (BMELV) “
- Sept 2009: Part of the organizing committee for the “1<sup>st</sup> DokMa Symposium 2009 “of the Evolutionary Ecology Department at the IFM-GEOMAR
- Feb 2007 - March 2008: Assistant at the Fisheries Biology, Institute of Marine Sciences (IFM-GEOMAR), Kiel
- Jan 2005 – Feb 2005: Assistant at the National Institute of Water and Atmospheric Research (NIWA) in Wellington, New Zealand participating in:  
- Sea Urchin research Project, NIWA Aquaculture Research Facility at Mahanga Bay  
- Oyster Disease testing program  
- Seaweed ecology project  
- Marine bio-security surveillance survey
- January 2004 – July 2004: Assistant at the Fisheries Biology, Institute of Marine Sciences (IFM-GEOMAR), Kiel

**CONFERENCES & WORKSHOPS:**

- May 2012: "6<sup>th</sup> World Fisheries Conference 2012", Edinburgh, Scotland
- Feb 2012: "Symposium on telemetry and data storage tags", at DTU AQUA Copenhagen, Denmark
- Nov 2011: "Bio-Resources from Oceans" Workshop, Berlin, Germany
- Sept 2011: "141<sup>st</sup> Annual Meeting of the American Fisheries Society", Seattle, United States
- Sept 2009: "ICES Annual Science Conference", Berlin, Germany
- April 2009: "1<sup>st</sup> ICES/ACOM Workshop on Age-reading in European and American eel (WKAREA)", Bordeaux, France

**RESEARCH CRUISES:**

- 13<sup>th</sup>/14<sup>th</sup> March 2012: K12-K13 – RV "ALKOR", Baltic Sea, fishery survey
- 8<sup>th</sup>-21<sup>st</sup> Apr 2011: AL 317 – RV "ALKOR", Baltic Sea, fishery survey

**PEER-REVIEWED PUBLICATIONS:**

Soares, M. , A. Biastoch, A., Harrod, C., Hanel, R., Marohn, L., **Prigge, E.**, Evans, D., Bodles, K., Behrens, E., Böning, C.W., Eizaguirre, C. Female philopatry and decline in European eel recruitment exposed by a highly dynamic North Atlantic circulation system (**under review**).

Marohn, L., **Prigge, E.**, Hanel, R. A long way down – Escapement success of silver eels from a German river system. *Freshwater Biology* (**under review**)

**Prigge, E.**, Marohn, L., Oeberst, R., Hanel, R. (2013). Model Prediction versus Reality – Testing the predictions of a European eel (*Anguilla anguilla*) stock dynamics model against the *in*

*situ* observation of silver eel escapement in compliance with the European Eel Regulation. ICES Journal of Marine Science, DOI:10.1093/icesjms/fss188

**Prigge, E., Marohn, L., Hanel, R. (2013).** Tracking the migratory success of stocked European eels (*Anguilla anguilla*) in the Baltic Sea. Journal of Fish Biology 82 (2), p. 686-699, DOI:10.1111/jfb.12032

**Prigge, E., Mahl Zahn, A., Zumholz K., Hanel, R. (2012).** Dietary effects on fatty acid composition in muscle tissue of juvenile European eel, *Anguilla anguilla* (L.). Helgoland Marine Research 66 (1), p 51-61, DOI: 10.1007/s10152-011-0246-3

Marohn, L., **Prigge, E.**, Zumholz, K., Hanel, R. (2009). Dietary effects on multi-element composition of European eel (*Anguilla anguilla*) otoliths. Marine Biology 156 (5), p. 927-933, DOI: 10.1007/s00227-009-1138-9

#### **ORAL PRESENTATIONS & POSTER (SCIENTIFIC CONFERENCES):**

**Prigge, E., Marohn, L., Oeberst, R., Hanel, R. (2012)** Model predictions vs. reality – Validation of the German management plan silver eel (*Anguilla anguilla*) escapement model. 6th World Fisheries Congress. Mai 7<sup>th</sup> - 11<sup>th</sup> 2012, Edinburgh, Scotland (Poster)

**Prigge, E., Marohn, L., Hanel, R. (2011)** Tracking migration routes of formerly stocked European eels (*Anguilla anguilla*) in the Baltic Sea. 141<sup>st</sup> Annual Meeting of the American Fisheries Society. September 04<sup>th</sup> - 08<sup>th</sup> 2011 Seattle, USA

**Prigge, E., Marohn, Hanel, R. (2010)** Lost in Migration? - Preliminary results of tracking migration routes of European eel (*Anguilla anguilla*) in the Baltic Sea. 1<sup>st</sup> PhD students conference. 4<sup>th</sup> - 6<sup>th</sup> October 2010, Hamburg, Germany (Poster)

#### **PUBLIC PRESENTATIONS:**

**Prigge, E (2011)** Gefahren für den Aal – Sterblichkeitsfaktoren in Binnengewässern. Public symposium “Der Aal – Ein Meeresbürger stirbt Aus” at Multimar Wattforum. 08<sup>th</sup> June 2011, Tönning, Germany

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## **ERKLÄRUNG**

Hiermit erkläre ich, dass die vorliegende Dissertation selbständig von mir angefertigt wurde. Die Arbeit ist unter der Einhaltung der Regeln guter wissenschaftlicher Praxis der DFG (Deutschen Forschungsgemeinschaft) entstanden. Diese Dissertation ist nach Form und Inhalt meine eigene Arbeit. Es wurden in der gesamten Arbeit keine anderen als die angegebenen Hilfsmittel verwendet. Ich habe diese Arbeit weder im Ganzen noch zum Teil einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein bisher erstes und einziges Promotionsverfahren.

Kiel, den \_\_\_\_\_

Enno Prigge