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RESEARCH ARTICLE

The European eel (*Anguilla anguilla*, Linnaeus), its lifecycle, evolution and reproduction: a literature review

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Abstract The European eel (*Anguilla anguilla* Linnaeus 1758) is a species typical for waters of Western Europe. Thanks to early expeditions on the Atlantic Ocean by the Danish biologist Johannes Schmidt who found small (<10 mm) leptocephali larvae in the Sargasso Sea about 100 years ago, we have now a strong indication where the spawning site for this species is located. The American eel (*Anguilla rostrata*, LeSueur) also spawns in the Sargasso Sea. The spawning time and location of both species have been supported and refined in recent analyses of the available historical data. Subsequent ichthyoplankton surveys conducted by McCleave (USA) and Tesch (Germany) in the 1980s indicated an increase in the number of leptocephali <10 mm , confirming and refining the Sargasso Sea theory of Johannes Schmidt. Distinctions between the European and American eel are based on morphological characteristics (number of vertebrae) as well as molecular markers (allozymes, mitochondrial DNA and anonymous genomic-DNA. Although recognised as two distinct species, it remains unclear which mechanisms play a role in species separation during larval drift, and what orientation mechanism eels use during migration in the open sea. The current status of knowledge on these issues will be presented. The hypothesis that all European eel migrate to the Sargasso Sea for reproduction and comprise a single randomly mating population, the so called panmixia theory, was until recently broadly accepted. However, based on field observations, morphological parameters and molecular studies there are some indications that Schmidt's claim of complete homogeneity of the European eel population and a unique spawning location may be an overstatement. Recent molecular work on European eel indicated a genetic mosaic consisting of several isolated groups, leading to a rejection of the panmixia theory. Nevertheless, the latest extensive genetic survey indicated that the geographical component of genetic structure lacked temporal stability, emphasising the need for temporal replication in the study of highly vagile marine species. Induced spawning of hormone treated eels in the aquarium was collective and simultaneous. In this work for the first time group spawning behaviour has ever been observed and recorded in eels. Studies in swim-tunnels indicate that eels can swim four to six times more

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efficiently than non-anguilliform fish such as trout. After a laboratory swim trial of eels over 5,500 km, the body composition did not change and fat, protein and carbohydrate were used in the same proportion. This study demonstrated for the first time that European eel are physiologically able of reaching the Sargasso Sea without feeding. Based on catches of newly hatched larvae, temperature preference tests and telemetry tracking of mature hormone treated animals, it can be hypothesised that spawning in the Sargasso Sea is collective and simultaneous, while presumably taking place in the upper 200 m of the ocean. Successful satellite tracking of longfin female eels in New Zealand has been performed to monitor migration pathways. Implementation of this new technology is possible in this species because it is three times larger than the European eel. In the future, miniaturisation of tagging technology may allow European eels to be tracked in time by satellite. The most interesting potential contribution of telemetry tracking of silver eels is additional knowledge about migration routes, rates, and depths. In combination with catches of larvae in the Sargasso Sea, it may elucidate the precise spawning locations of different eel species or groups. Only then, we will be able to define sustainable management issues by integrating this novel knowledge into spawners escapement and juvenile fishing quota.

Keywords *Anguilla* · Migration · Sargasso Sea · Molecular studies · Spawning behaviour · Satellite

Introduction

Although a large amount of scientific literature has been produced on freshwater eels (*Anguilla* sp.; see e.g. references of this review), major questions still have to be resolved mainly on the topic of spawning grounds and reproduction. Already around 350 BC Aristotle wrote in his '*Historia Animalium*': ''*the eels come from what we call the entrails of the earth. These are found in places where there is much rotting matter, such as in the sea, where seaweeds accumulate, and in the rivers, at the water's edge, for there, as the sun's heat develops, it induces putrefaction*.'' (Bertin 1956). Until the early 20th century, one could reasonably speak of the *mysterious* life of the eel. Thanks to the early marine expeditions of the Danish biologist Johannes Schmidt (see Fig. 2 for sampling stations for larvae) the central mystery of its breeding location has been elucidated (Schmidt 1922, 1923, 1925, 1935). Schmidt based his conclusion regarding the spawning site of the European eel in the Sargasso Sea (Fig. 1) on larvae (Lepocephali) distributions (see Section ''The location of the spawning areas'').

Despite the intensive research on eels following the work of Schmidt (1923, 1925, 1935), there are many uncertainties, and there is still a lack of knowledge on many aspects of the life cycle of the European eel. This is best summarised in the book of Harden Jones (1968): ''*No adult eels have ever been caught in the open Atlantic nor eggs definitely identified in the wild. Migration routes and spawning conditions for adults are unknown or conjectural, as are many details of the development, feeding and growth of larvae. Mechanisms for species separation (note: separation between the American eel and the European eel) during larvae migration are speculative, and details of larval migration or drift are uncertain*''.

In this review we will present the progress in knowledge and new insights about the eel life cycle following the initial work of Schmidt at the beginning of the previous century. This new information is based on the application of new techniques and methodologies such as refined and improved catching techniques for ichthyoplankton surveys, new molecular DNA analyses, telemetry-tracking studies, endocrinological surveys in field studies, energy balance studies in large swim-tunnels, and behavioural studies of hormone treated animals.

Eel life cycle and fisheries

The life-history of the European eel (*Anguilla anguilla* L.) depends strongly on oceanic conditions; maturation, migration, spawning, larval transport and recruitment dynamics are completed in the open ocean (Tesch 2003). Partially mature adults leave the continental rivers at different

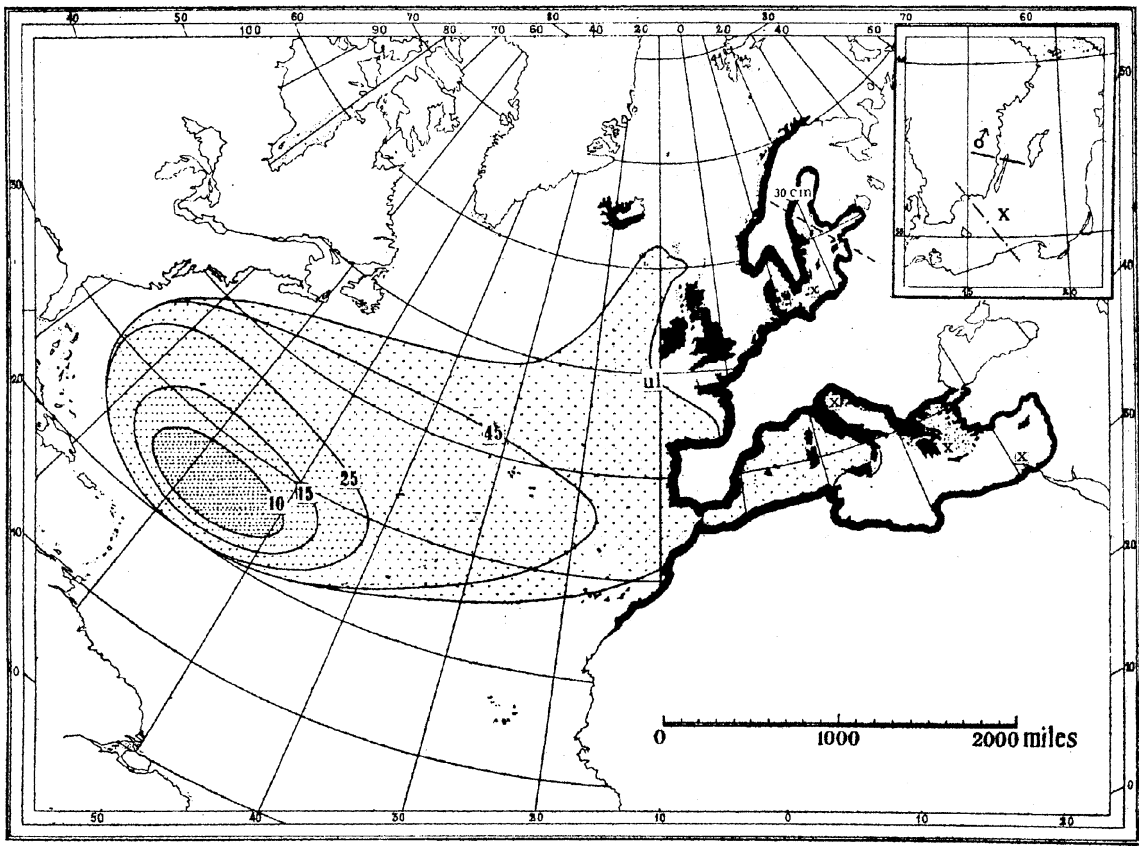

Fig. 1 Distribution patterns of eel larvae with the size of the larvae in mm (source: Schmidt 1923)

times, strongly dependent on lunar phase and atmospheric conditions (Desaunay and Guérault 1997; Okamura, Yamada, Tanaka, Horie, Utoh, Mikawa, Akazawa, Oka 2002; Tesch 2003), swim southward using the Canary and North-equatorial currents and arrive 6–7 months later at the Sargasso Sea to spawn and then die. The leptocephali larvae are transported along the Gulf Stream and North-Atlantic Drift for a journey of 8–9 months back to the eastern Atlantic coast (Lecomte-Finiger 1994; Arai et al. 2000), where they metamorphose to glass eels, ascent rivers and grow till partial maturity, 6–10 years later (Tesch 2003).

A total of 25,000 tons of eels are consumed in Europe annually (Usui 1991). Eel fisheries in Europe cover an area of 90,000 km^2 with approximately 25,000 people generating income from eel fisheries and aquaculture (Dekker 1998, 2003a, 2004). On a worldwide scale eel (fisheries and fish culture) was estimated to produce between 100,000 to 110,000 tons in 1987, which corresponds to approximately 2 to 2.2 billion Euros per year (Heinsbroek 1991).

Eel populations have been declining worldwide over the last decade (Stone 2003). European eel (*Anguilla anguilla*) numbers have dropped as much as 99% since the early eighties of the previous century, while Japanese eel (*Anguilla japonica*) dropped as much as 99% since the early seventies of the previous century (Dekker, 2003b). North-American eels are suffering steep drop-offs as well (Fig. 3a).

Also the trends in glass eel recruitment to the European continent show steep declines from the eighties of the previous century (Fig. 3b).

The exact cause for this phenomenon is unknown, but possible causes include: (a) contamination with toxic PCBs, which are released from fat stores during their long-distance migration and interfere with reproduction (Castonguay et al. 1994); (b) infection with the swimbladder parasite *Anguillicola crassus* (Haenen 1995); (c) viruses

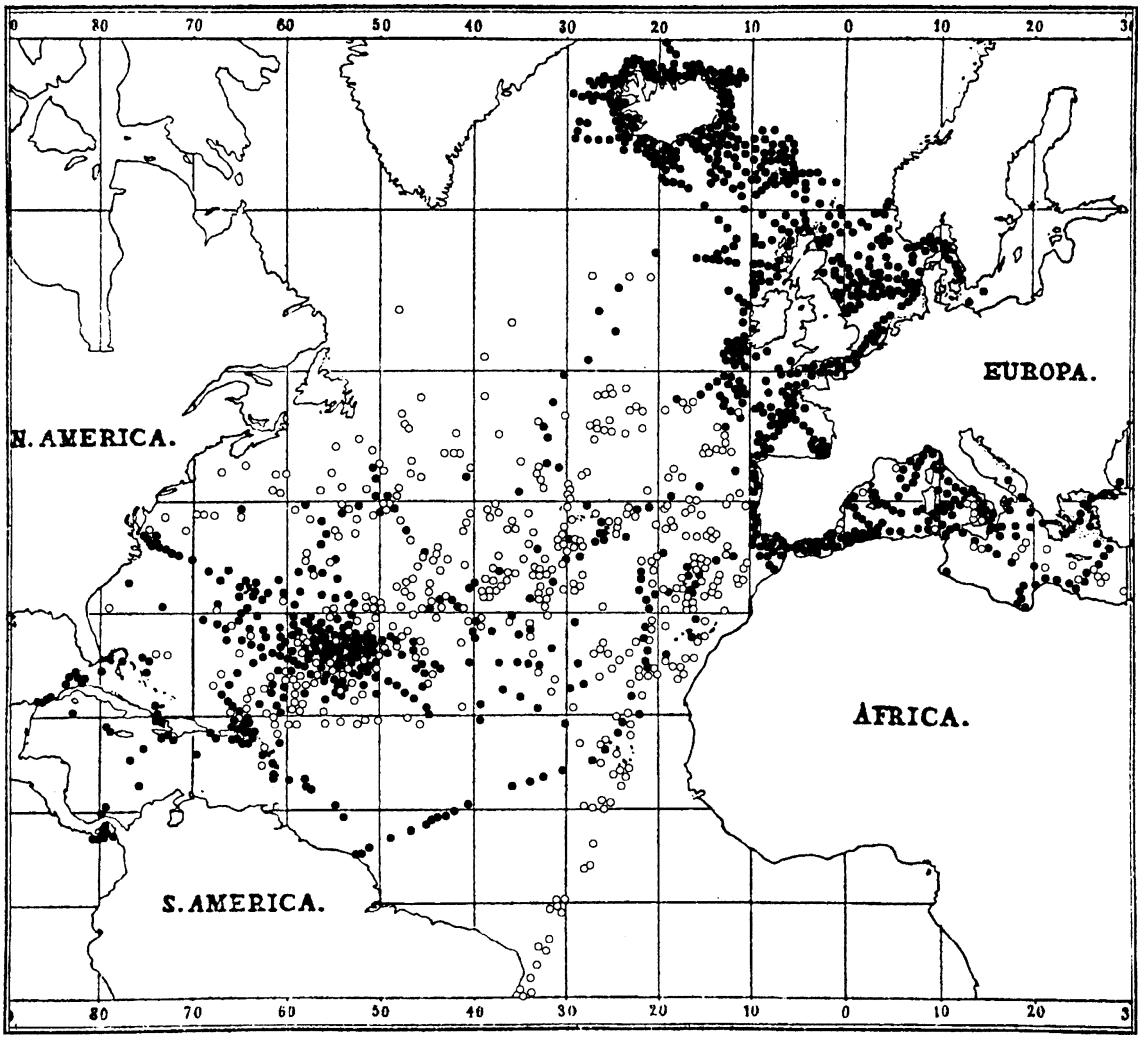

Fig. 2 Principal Danish collection stations of eel larvae, 1903–1922 (After: Schmidt 1925). Closed circles indicate stations by research ships and open circles those by other ships (source: Vladykov 1964)

(van Ginneken et al. 2004, 2005a), (d) oceanographic/climatic changes (Knights 2003); (e) diminished fat stores due to insufficient food supplies in the inland waters (Svedäng and Wickstrom 1997); (f) blockage of migration routes by power stations and plants (Castonguay et al. 1994); and (g) over-fishing (Castonguay et al. 1994; Dekker 2003a, 2004).

The location of the spawning areas

Information about the exact location of the spawning grounds can be acquired based on catches of larvae eels in relation to size and age. Johannes Schmidt gathered records of over 10,000 European eel larvae and about 2,400 American eel larvae over a period of 25 years. Schmidt based his conclusions about the oceanic life history of eels on the spatio-temporal distribution of larvae of different sizes. He never captured adult eels in the open ocean en route to or in the Sargasso Sea. Furthermore, eel eggs still have not been identified in plankton samples from the Sargasso. Schmidt reached the conclusion that the European eel only spawns in the Sargasso Sea in the south-western portion of the North Atlantic Ocean from the distribution of the smallest larvae (Schmidt 1923).

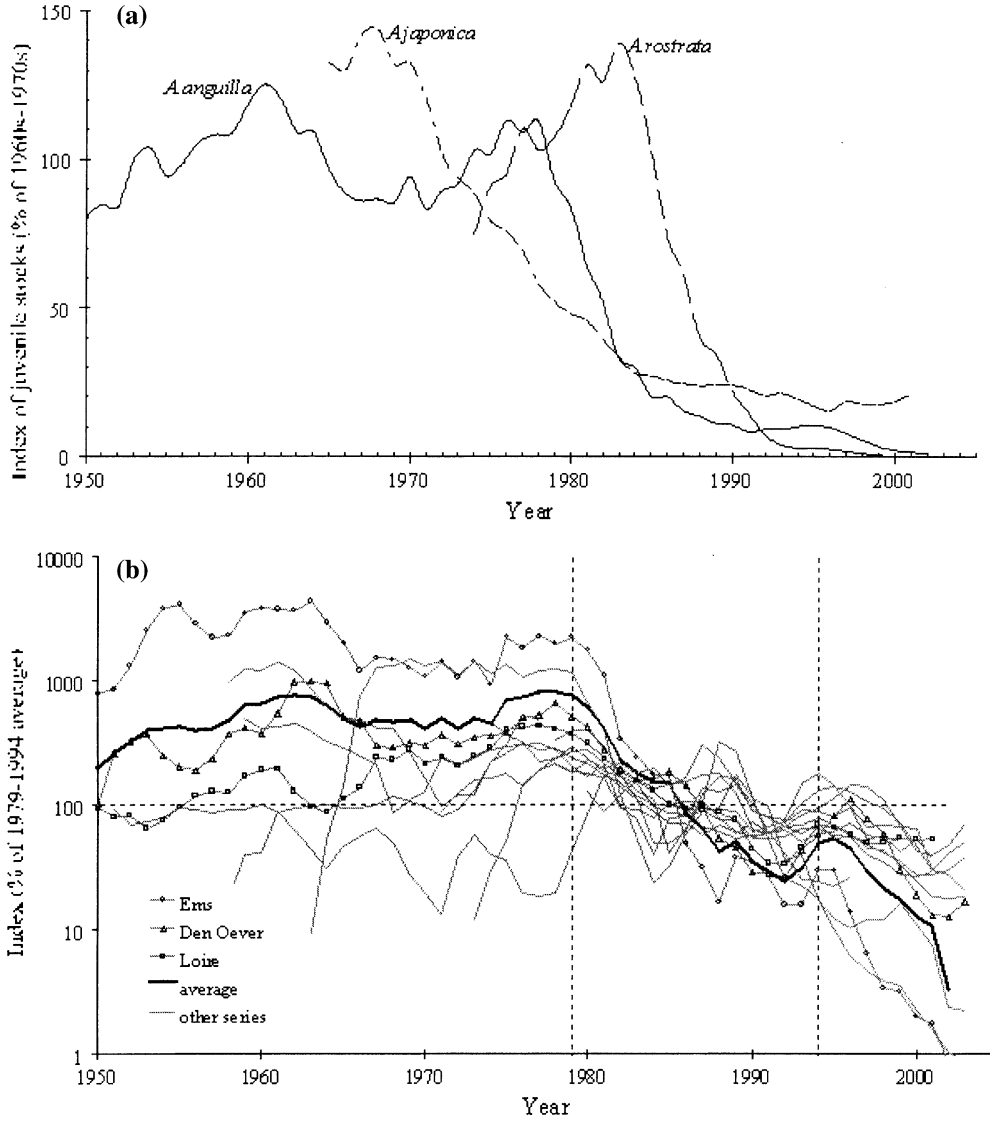

Fig. 3 (**a**) Time trends in juvenile abundance of the major eel stocks of the world. For *Anguilla anguilla*, the average trend of the four longest data series is shown; for *A. rostrata*, data represent recruitment to Lake Ontario; for *A. japonica*, data represents landings of glass eel in Japan (Source: Dekker 2003b, 2004). (**b**) Trends in glass eel recruitment to the continent. Individual data series are given in grey; common trend (geometric mean of the three longest data series in black. Data from ICES (2004) and Hagström and Wickström (1990) (source: Dekker 2004)

This until recently well-accepted conclusion about a single spawning area in the Sargasso Sea for the European eel—is currently under discussion based on recent molecular studies and may need to be critically revised (see Section ''The possibility of multiple spawning areas within and outside of the Sargasso Sea, Molecular arguments'').

Schmidt also concluded that the American eel spawned in an overlapping area to the west, but he had records of only 22 larvae <10 mm long (Schmidt 1925). Although there are substantial weaknesses to Schmidt's claim (Boëtius and Harding 1985) and despite the limitations of his data, Schmidt's conclusions about eels life history are essentially correct and the Sargasso Sea appears to be the primary spawning area for most North-Atlantic eels (American and European). Johannes Schmidt also stated that the peak of

European eel spawning was in April and that the spawning area is centred to the Northeast of the spawning area of the American eel, which has its spawning peak in February (Schmidt 1925). The times and areas of eel spawning have been supported and refined through recent analyses of the available historical data by Boëtius and Harding (1985), Kleckner and McCleave (1982, 1985) and McCleave et al. (1987). Ichthyoplankton surveys conducted by a group led by McCleave (USA) and a group led by Tesch (Germany) in the 1980s expanded the number of leptocephali <10 mm collected at sea (Tesch 1982; Schoth and Tesch 1982; Wippelhauser et al. 1985; Castonguay and McCleave 1987; McCleave and Kleckner 1987; Kleckner and McCleave 1988; Tesch and Wegner 1990). The collection now comprises more than 700 American eel leptocephali and more than 1600 European eel leptocephali <10-mm long (McCleave et al. 1987). All catches of American eel leptocephali <7 mm total length (188 specimens) were obtained within a broad ellipse extending eastward from the Bahamas to about 58° W longitude. All catches of European eel leptocephali <7 mm long (226 specimens) were obtained within a narrow overlapping ellipse. The distribution of American and European eel larvae <7.5 mm TL is limited to the north by the boundary between warm saline surface water of the southern Sargasso Sea and a mixed convergence zone of water. Larvae <7 mm TL are accepted as an indicator of spawning during the preceding three weeks, which is based upon assumed length at hatching and a growth curve developed from artificial maturation experiments in the laboratory (Yamamoto and Yamauchi 1974; Yamauchi et al. 1976).

Based on all these observations, we now know that the European eel spawns primarily from March to June within a narrow ellipse whose long axis extends east–west from approximately 48° to 74° W longitude between 23° and 30° N latitude and that the American eel spawns primarily from February to April within a broader oval between approximately 52° and 79° W longitude and 19° and 29° N latitude (McCleave et al. 1987). So spawning of the European and American eel species is partially sympatric in space and time (McCleave et al. 1987). Continental separation of the two species is probably ensured by initial distributional bias from partially allopatric spawning and by different developmental rates (Tesch 2003). Differences in vertical migration between the leptocephali of the two eel species can partly explain how *Anguilla rostrata* detrains from the Gulf Stream to invade the North American coast, while *Anguilla anguilla* presumably stays in the stream on its way to Europe (Castonguay and McCleave 1987). Social interactions and the existence of a species-specific pheromone (McCleave 1987) may help prevent interbreeding. Our observations of spawning behaviour in hormone treated European eels in a 4,000-liter aquarium strengthen the probability that spawning is triggered by pheromones (Section ''Spawning behaviour and reproduction'').

Based on the distribution of newly hatched leptocephali, it is believed (Kleckner et al. 1983; McCleave and Kleckner 1985; McCleave et al. 1987) that adults of both species spawn in, and to the south of, a persistent, meandering, near-surface frontal zone that stretches east–west across the Sargasso Sea (Voorhis and Bruce 1982). This is the so-called subtropical convergence zone (STCZ), a region where the colder water of the northern Sargasso Sea meets the warmer water of the southern Sargasso. This natural boundary divides the surface waters of the Sargasso Sea into distinct northern and southern water masses (Katz 1969; Voorhis 1969; Kleckner et al. 1983).

There are sharp fronts in the STCZ, with shingles of 100–300 km length, separating water masses in the subtropical frontal zone. These fronts act as a boundary for many organisms and some feature of the frontal zone or the southern waters, such as odour or temperature, may serve as signals to migrating eels to cease migrating and spawn (Kleckner et al. 1983; McCleave 1987; McCleave et al. 1987). Earlier work of a German group corroborates these results (Schoth and Tesch 1982; Wegner 1982).

For *Anguilla* larvae, leptocephali are much more abundant on the south face of the front that separates the two general water masses in the STCZ (Kleckner and McCleave 1988; Tesch and Wegner 1990). Greater abundances of larvae from other families of shelf eel species*(Chlopsidae, Congridae, Moringuidae, Muraenidae and*

Ophichthidae) and other fish species have been found at or south of fronts in the STCZ of the Sargasso Sea (Miller 1995).

It is hypothesised that differences in species composition are caused by a marked decrease of primary production south of the front (Kleckner et al. 1983; Miller 1995). This reduction in primary productivity, combined with the seasonal stability of this layer, may provide a variety of persistent olfactory cues, distinct from those of the northern water mass, providing olfactory signals to eels returning to spawn after many years in freshwater. It is possible that the homing mechanism of adult eels may be based on a similar mechanism to that found in Atlantic salmon, imprinting on odours and tastes of the waters of the southern Sargasso Sea. For sexually immature eels it has been demonstrated that their olfactory senses are highly developed. They are capable of detecting chemical compounds (such as β-phenylethanol) at dilutions as low as $1{:}2.85\times10^{18}$ (Teichmann 1959).

In an experiment, the estuarine migration of anosmic and control silver-phase American eels was examined during spawning migration in fall. Control eels moved more rapidly, using tidal properties to leave the estuary. In contrast anosmic eels took a longer time to leave the estuary and they were unable to use tidal stream transport for movement out of the estuary (Barbin et al. 1998). From these observations it can be concluded that olfaction plays an important role at (initial) migration in adult eels.

Another possibility is that a temperature gradient in the surface waters of the frontal zone as high as 2°C per km (Voorhis 1969) could act as a triggering or orientation mechanism. From our swim experiments we obtained data regarding the swim potential of eels (Section ''Swimming capacity of swimming eels''). Thus we can assume that an eel with a size of 1 m and swimming speed of approximately 1 body-length (BL) per second could experience a temperature difference less than 0.002°C per second. Based on telemetry observations of diurnal migration patterns of migrating silver eels with correspondingly larger temperature fluctuations, it seems unlikely that temperature acts as orientation cue (Tesch 1978, 1989).

Recently, we studied the orientation of yellow (non-migratory) female eels in a freshwater pond to the earth's magnetic field by means of microchips injected into their muscle (van Ginneken et al. 2005b). Detectors for microchips were mounted in tubes placed in the pond to determine if eels orientated themselves with respect to earth's magnetic field. There was a seasonal component in the orientation mechanism, with a significantly lower preference for specific orientation in summer compared to fall. A preference for tubes orientated in a south–southwest direction (the direction of the Sargasso Sea) in fall suggested orientation to the earth's magnetic field may play a role in migration in eels (van Ginneken et al. 2005b).

Leptocephali transport

The migration of leptocephali from the area of the Sargasso Sea to the continental shelves and coastal water is very complex and cryptic, foremost because of an incomplete understanding of elements of the physical environment which contribute to variability in ocean transport like recirculation, meandering, eddy formation and tides (McCleave 1993). Secondly, most leptocephali undergo daily and ontogenetic vertical migrations (Schoth and Tesch 1984; Castonguay and McCleave 1987). The latter term indicates that leptocephali undergo changes in vertical distribution with age. Thirdly, we do not know whether the transport of European leptocephali larvae across the Atlantic is based on passive and/or active processes, depending on the larval developmental stage. Schmidt (1925) provided little information on vertical distribution of leptocephali of the American and European eel in the Sargasso Sea. He stated only that larvae 7–15 mm long were found between 75 and 300 m deep, whereas 25 mm larvae were found in the water layer between the surface and 50 m. Studies performed more recently, indicated that *Anguilla* leptocephali <5 mm long did not exhibit a diel vertical migration, as they were distributed between 50 m and 300 m both by day and night (Castonguay and McCleave 1987). *Anguilla* of the

length range 5–19.9 mm mostly occurred between 100 m and 150 m by day and between 50 m and 100 m by night (Castonguay and McCleave 1987). While *Anguilla* >20 mm were found deeper than *Anguilla* <20 mm by day, between 125 m and 275 m, and mostly between 30 m and 70 m by night (Castonguay and McCleave 1987). This pattern of migration at shallow warm depths at night and diving to deeper, colder depths during day (probably to avoid high light intensities) has been confirmed in another study west of the European continental shelf (Tesch 1980). In this study the depth preference of leptocephali during daylight was 300–600 m, and at night 35–125 m (Tesch 1980). Based on these diurnal patterns of larvae distribution it can be concluded that larvae <5 mm have no active transport mechanism while from a size of >5 mm on active movement may play a role. Also based on morphological parameters, active swimming of larvae <5 mm can be excluded, because they are so primitive at hatch that an effective swimming mechanism can be excluded (Yamamoto and Yamauchi 1974; Yamauchi et al. 1976, Pederson 2003, Palstra et al. 2005).

Therefore, it is assumed that *Anguilla* larvae <5 mm were probably spawned no more than 7 days prior to capture and the depth of catch can be indicative of the spawning depth of the adults. The water of the Sargasso is 5 km deep, but spawning probably takes place in the upper few hundred meters. This is not only based on the depth of catch of <5 mm larvae, but also on the release of hormone treated European and Japanese adult female eels with telemetry transmitters (see Section ''Migration and spawning depth'').

Although the circulation patterns and oceanic currents are complex and poorly understood, some information is available on the transport of leptocephali larvae out of the Sargasso Sea area with movements toward coastal areas. Discontinuities in the assemblages of *Anguilla* within and among transects suggest that convergence of surface water toward fronts in the STCZ may concentrate leptocephali close to the fronts and that frontal jets may transport leptocephali eastward (Miller and McCleave 1994). The size distributions of leptocephali suggest that gyres in the south-western Sargasso Sea, an Antilles Current, and the Florida Current north of the Bahamas are routes of exit for *anguillid* eels. Most leptocephali enter the system north of the Bahamas rather than through the Straits of Florida or island passages (Kleckner and McCleave 1982; McCleave and Kleckner 1985). A previously hypothesised persistent Antilles Current sweeping north-westward along the eastern edge of the Bahamas is no longer believed to exist (Olson et al. 1984). The most important transport mechanism of leptocephali westward toward the northern Bahamas is a gradual advection mechanism. The other transport pathway, which is of minor importance, is southward toward Hispaniola on circulation mechanisms described by Olson et al. (1984).

Most of the juvenile eels entering European waters are European eels, but less than 1% are American eel, judged by vertebral counts (Boëtius 1980). It is not known how many European eels colonise the American continent. Given the overlap in spawning period and spawning grounds of American and European eels (McCleave et al. 1987; Tesch and Wegner 1990) a substantial fraction of leptocephali of both must be subjected to similar advective processes in the North Atlantic. Therefore, it is unclear what mechanism is the basis for the split between the two species distributing only such a small fraction of leptocephali to habitats outside of their continent of origin. It is possible that there is a clear genetically determined active choice of the water currents used by the larvae (Kleckner and McCleave 1985). Another possibility is a strict, genetically determined period of metamorphosis (Power and McCleave 1983; McCleave 1993; Cheng and Tzeng 1996), which ultimately brings the larvae into contact with the different currents flowing to the American or European continent. Clear differences in metamorphose time and capabilities between the two species have been reported (Kleckner and McCleave 1985; van Utrecht and Holleboom 1985). American eel leptocephali may become developmentally capable of undergoing metamorphosis after 6–8 months and remain viable for 4–6 months (Kleckner and McCleave 1985). In contrast, European leptocephali become capable of metamorphosis only after about 18 months, but remain viable for several years (van Utrecht and Holleboom 1985). New

knowledge about timing of metamorphosis is available in Lecomte-Finiger (1994) and Arai et al. (2000). According to Lecomte-Finiger (1994) the mean age of glass eel ranged from 190 to 280 days. The calculated growth rate was 0.26–0.30 mm per day. Thus, European eel larvae spend less than 1 year in transatlantic migration (Lecomte-Finiger 1994) in contrast to the earlier estimated period of 2–3 years (Schmidt 1922).

Arai et al. (2000) gave more detailed information based on Otholith microstructure and microchemistry. Otholith increment width markedly increased from age 132 to 191 days (156 ± 18.9 days; mean ± SD) in *A. rostrata* and 163 to 235 days (198 ± 27.4 days; mean ± SD) in *A. anguilla*. The duration of metamorphosis was estimated to be 18 to 52 days from otholith microstructure, for both species studied. Age at recruitment were 171 to 252 days (206 ± 22.3 days; mean ± SD) in *A. rostrata* and 220 to 281 days (249 ± 22.6 days; mean ± SD) in *A. anguilla* (Arai et al. 2000).

Currently there are two theories about larval transport from the spawning area to the coastal habitats of different continents. One theory suggests a passive multi-year and variable oceanic transport (van Utrecht and Holleboom 1985; Guérault et al. 1992). The other theory states that larvae transport is an active process of short duration, including the time of metamorphosis of European eels of only 7–9 months (Lecomte-Finiger 1994; Arai et al. 2000 see also Section ''The location of the spawning areas''). It is difficult to choose between the multi-year passive and active larvae transport theories due to problems that arise from the interpretation of glass eel otholiths. There are conflicts about the accuracy of ageing glass eels using SEM (Scanning Electron Microscope) otholithometry. In general it is suggested that there is a relationship between Otholith increment deposition and somatic growth. This method was used by Lecomte-Finiger (1994) to state that migration of glass eels from the Sargasso Sea was an active and not a passive process. However, in practice the matter is more complicated. A first methodological problem is that light microscopy can not resolve objects separated by less than 0.2 μm (Campana and Neilson 1985), so they cannot be used to count zones in the so called ''B-type'' otholiths. B-type otholiths are probably from slow growing animals without clear regular incremental separations. Increments of around 1.9 μm are found in normal growing animals with so-called ''A-type'' otholiths (Umezawa and Tsukamoto 1991). A second problem is that despite the close relationship between increment counts and body growth, other factors also may affect the size and deposition of otholith increments, such as water temperature, feeding ration, feeding frequency, starvation and photoperiod (for references see Umezawa and Tsukamoto 1991). Catadromous fish species such as eels and their larvae may experience enormous differences in food supply, temperature, salinity etc. during their seaward migration. Therefore information about growth rates for leptocephali of both American and European eel has to come from growth studies under optimal standardised conditions. Luckily, Pedersen (2003) and the Leiden research group (Palstra et al. 2005) have succeeded in the production of leptocephali of the European eel allowing the development of clinical/assessment of growth rates under experimental conditions.

The possibility of multiple spawning areas within and outside of the Sargasso Sea

The hypothesis that all European eels migrate to the Sargasso Sea for reproduction and constitute a single randomly mating population, the so-called panmixia theory, is generally accepted. However, based on field observations (Grassi 1896; Bast and Klinkhardt 1988; Lintas et al. 1998), morphological parameters, such as the total number of vertebrae (Boëtius 1980; Harding 1985), and recent molecular work (Lintas et al. 1998; Bastrop et al. 2000; Daemen et al. 2001; Wirth and Bernatchez 2001; Maes and Volckaert 2002), there are some indications that the European eel population is genetically diverse, pointing to discrete spawning populations. Nevertheless, the latest extensive genetic survey indicated that the geographical component of genetic structure lacked temporal stability, emphasising the need for temporal replication in the study of highly vagile marine species (Dannewitz et al. 2005). Hence, indications for one single as well as several discrete spawning sites

have been provided in the last century, which will be discussed in this section.

Classical arguments

In the 1960's, Tucker (1959) and D'Ancona (1960) hypothesised that eel spawning areas could be located in the Mediterranean close to the Strait of Messina (a 2000 m deep-water body in the south of Italy). This assumption was based on the lack of any catch of a migrating maturing eel in the narrow Strait of Gibraltar despite considerable research efforts (Ekman 1932). In contrast, migrating silver eels have been caught in the Sont (the narrow Sea Strait of 4.5 km width in Denmark connecting the North Sea and the Baltic Sea) and the Strait of Dover (Tucker 1959). Additionally, only one maturing eel with a Gonado-somatic Index (GSI) of 10 has been caught west of Morocco, close to the Azores (Bast and Klinkhardt 1988), which may point to the existence of another spawning area located west of Morocco. However, conclusions based on sporadic catch data remain highly speculative and to date no serious attempts have been made to catch eels in the open Atlantic (see Section ''Tracking silver eel migration'').

There are several further ''traditional'' arguments against the single spawning site theory:

(a) Grassi and Calandruccio discovered in 1896 in the Strait of Messina leptocephali larvae of 50 mm, which they ascribed to the larval stage of the European eel (Grassi 1896).
(b) Some authors reported the presence of adults with enlarged eyes (an indication for advanced sexual maturity) in the Strait of Messina (Lintas et al. 1998).
(c) A re-evaluation of the total number of vertebrae (TNV) in European eel samples collected by Johannes Schmidt demonstrated that Schmidt's claim of homogeneity of the eel population and a unique spawning location was an overstatement (Harding 1985). The number of vertebrae increased on a North-South latitudinal gradient along the Atlantic coast. In the Mediterranean, a significantly heterogeneous distribution in TNV was observed, without any apparent geographical cline. Harding (1985) suggested at least two, possibly three, distinct groups, each with their own distribution of length and total numbers of vertebrae. Environmental influences in the early life phase of larvae, including their origin in separate parts of the spawning area and different migration routes to the European coasts could, however, result in similar trends (Harding 1985).
(d) Very young glass eel have been observed along the Atlantic coast, from Morocco to the Netherlands and in the Western Mediterranean (Lecomte-Finiger 1994). This may be indicative of spawning areas west of Morocco, closer to the European continent than the Sargasso Sea.

On the other hand, ''traditional'' arguments in favour of the single spawning site theory include:

(a) No spawning adults have ever been observed in the Mediterranean Sea (note: this is also the case in the Sargasso Sea).
(b) Eels are rarely observed in the Black Sea, which is not expected if separate eel populations would spawn in the Mediterranean Sea.
(c) The number of vertebrae of eels from the Atlantic corresponds to that of eels from the Mediterranean (Tesch 2003).
(d) The Mediterranean contains only leptocephali larvae >60 mm long.
(e) These larvae become larger from the west of the Mediterranean to the east.
(f) Coherence in recruitment patterns gave no evidence for any subdivision of the European eel stock (Dekker 2000).

Molecular arguments

Molecular data have also provided both evidence supporting and rejecting the Panmixia hypothesis using various genetic markers. They will be reviewed chronologically to provide an overview of the shifts in ideas, along with the continuous development of new molecular markers.

Early population genetic studies, based on observed differences in transferrines and liver esterases, claimed that European eel populations differed between several continental European locations (Drilhon et al. 1966, 1967; Drilhon and Fine 1968; Pantelouris et al. 1970), suggesting that eels in the south-eastern part of the Mediterranean formed a separate group and reproduce in this area. This supported the theory of discrete populations, although differential selection was also proposed as a possible explanation (Pantelouris et al. 1970, 1971). However, the conclusions of most allozyme-based studies from the 1960s have been re-evaluated and rejected on methodological grounds (Koehn 1972). Later allozymatic studies failed to detect obvious spatial genetic differentiation (de Ligny and Pantelouris 1973; Comparini et al. 1977; Comparini and Rodinò 1980; Yahyaoui et al. 1983).

Studies based on mitochondrial DNA initially provided only limited insights into the geographical partitioning of genetic variability in European eel, mainly because of the very high number of haplotypes in the D-loop region and the expected recent timescale of intraspecific differentiation (Lintas et al. 1998). The study of Lintas et al. (1998) supports the genetic homogeneity of the European eel population. They sequenced the 5′ end the mitochondrial D-loop of 55 eels caught at different European locations, known to show high levels of nucleotide substitutions among teleosts (Lee et al. 1995). Nevertheless, Lintas et al. (1998) found so little DNA differentiation among European eel individuals from distant geographical locations, that they suggested all European eels being derived from a common genetic pool. A recent study by Bastrop et al. (2000) confirmed this result based on 16sRNA sequences. Although the European eel population is genetically more diverse than the American eel population (Avise et al. 1986; Bastrop et al, 2000) and the genetic homogeneity of the European eel seemed beyond dispute according to these recent molecular DNA studies (Lintas et al. 1998; Bastrop et al. 2000), the possibility remained of multiple spawning areas. Lintas et al. (1998) hypothesised two situations in which the European eel would remain genetically homogeneous with the existence of several discrete spawning areas:

(1) A partial reproductive isolation with some gene flow between eels from the Mediterranean and the Sargasso Sea.
(2) Other spawning sites than the Sargasso Sea with mixing of larvae originating from different breeding areas.

Panmixia in the European eel became thus widely accepted until three independent recent genetic studies reported evidence for a weak but significant population structure (Daemen et al. 2001; Wirth and Bernatchez 2001, Maes and Volckaert 2002). New indications of the non-random distribution of haplotypes were reported using the less variable cytochrome *b* mtDNA marker (Daemen et al. 2001). European eel populations exhibited much lower haplotype diversity at the cytochrome *b* locus compared to the 5′ end of the D-loop (Lintas et al. 1998). The genetic variation observed at the cytochrome *b* locus was nevertheless high (17 haplotypes in 107 eels), with two central haplotypes in the haplotype network and a significant latitudinal clinal pattern of cytochrome *b* haplotypes fitting an isolation-by-distance model. Further, Daemen et al. (2001) detected a weak but significant genetic differentiation among the British/Irish, Atlantic, Moroccan, Italian and Swedish Baltic populations, respectively, using five nuclear microsatellite loci. In a later study, Wirth and Bernatchez (2001) also identified weak but highly significant genetic structure in the European eel population among 13 samples, based on seven microsatellite loci, reporting evidence for isolation-by-distance (IBD) (Fig. 4b). Finally, Maes and Volckaert (2002) reported clinal genetic structure and IBD in the European eel population using 15 allozyme loci and identified three distinct groups: Northern Europe, Western Europe and the Mediterranean Sea.

Results from the former genetic studies pointed to the existence of a genetic mosaic in the European eel, consisting of several isolated spawning groups. According to Wirth and Bernatchez (2001), and Maes and Volckaert (2002), in theory three models can explain the rejection of the panmixia hypothesis:

(a) There is one common spawning area, but there is a temporal delay between the arrival

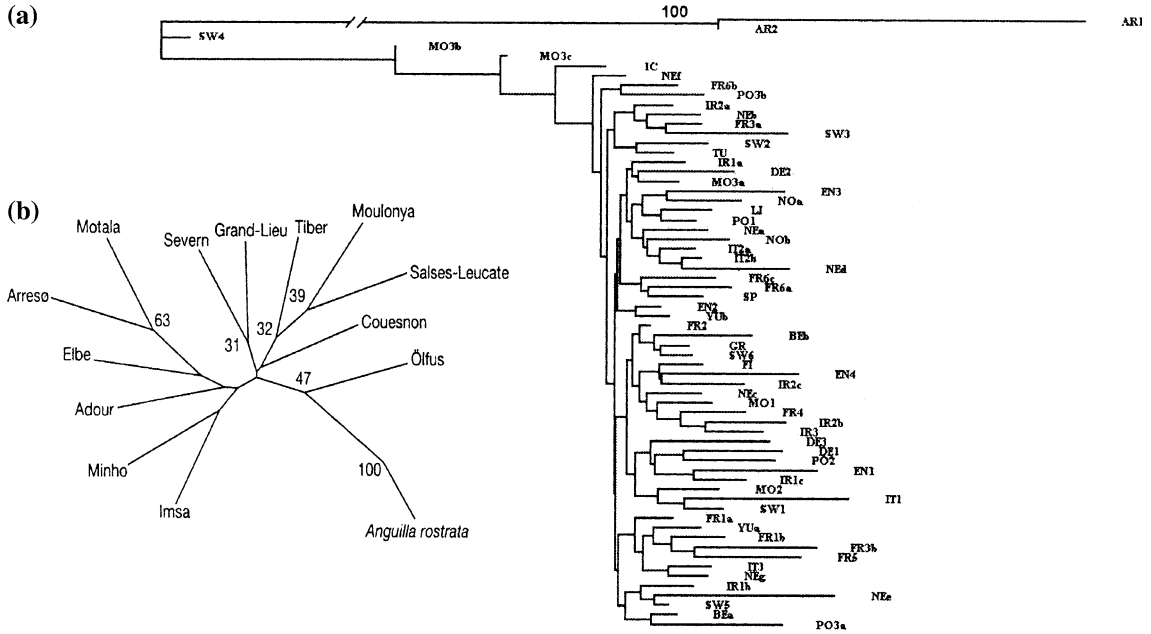

Fig. 4 Genetic evidence based on microsatellites in favour of and against the Panmixia hypothesis using (**a**) combined geographical and temporal (Dannewitz et al. 2005) or (**b**) exclusively geographical (Wirth and Bernatchez 2001) samples across Europe

of adult eels originating from different latitudes.

(b) There is one reproductive area used by different populations where different sea currents carry the leptocephali back to their parent's original freshwater habitat.

(c) There is only one shared spawning area where assortative mating occurs and larval homing to parents' habitat takes place using an unknown mechanism.

Finally, the most recent and extensive genetic study on European eel increased significantly the geographical sampling (42 sites) and included crucial temporal replicates (at 12 sites) into their analyses to check for consistency in the observed spatial pattern (Dannewitz et al. 2005). Surprisingly, no stable spatial genetic structuring was detected anymore, while temporal variance in allele frequency exceeded well the geographical component (Fig. 4a). Possible sampling bias due to life stage mixing and a lower effective population size than expected could explain these conflicting results (Dannewitz et al. 2005).

In summary, nuclear and mitochondrial DNA data provided evidence for a subtle heterogeneous European eel population, with a minimal geographical component across Europe, but with most genetic variation being present between temporally separated populations. Such results reflect the high variance in reproductive success in marine species in general, inducing small and large-scale temporal changes in genetic composition between cohorts (Dannewitz et al. 2005; Maes 2005; Pujolar et al. 2005b).

Evidence of a single or multiple spawning sites in other Anguilla spp.

Similar results of lack of differentiation were observed in several other eel species. The American eel (*A. rostrata*) showed no evidence for a geographical subdivision, with the exception of clinal allozyme variation putatively imposed by selection (Williams et al. 1973; Koehn and Williams 1978; Williams and Koehn 1984; Avise et al. 1986, Wirth and Bernatchez 2003). These data suggested that *Anguilla rostrata* is genetically homogenous, forming a single randomly mating population. In the Japanese eel (*Anguilla japonica*), no evidence was found of genetic structure over large geographic areas in studies

based on mitochondrial DNA (Sang et al. 1994; Ishikawa et al. 2001), but clinal variation was observed at allozymes (Chan et al. 1997). In *A. australis* and *A. dieffenbachii*, an allozyme based study showed a signal of differentiation between recruiting and resident populations (Smith et al. 2001). In the giant mottled eel (*A. marmorata*), even several genetically isolated populations could be detected using mtDNA (Ishikawa et al. 2004). Intra-specific divergence was of the same level as the lowest inter-specific divergence in the genus *Anguilla* between the North-Atlantic eels or between the sub-species of *A. bicolor*. The distribution pattern of five populations was closely associated with the water-mass structure of oceans and major current systems. This observation suggests that present population differentiation in *A. marmorata* might have resulted from the establishment of new population specific spawning sites in different oceanic current systems as the species colonised new areas (Tsukamoto et al. 2002; Ishikawa et al. 2004).

Evolutionary consequences of the European eel's life-history traits

After consideration of all arguments from the traditional and molecular studies, we are able to summarise and extend some conclusions in favour or against the panmixia hypothesis. Several life cycle characteristics in the European eel may or may not contribute to genetic structuring:

(a) Age at maturity is highly variable, ranging from 6 to 50 years in females (Poole and Reynolds 1998) over a latitudinal gradient. In Northern Europe the mean age at maturation of females can range from 12 to 20 years (or older), while in Southern Europe it is 6–8 years (Tesch 1977). If there is a temporal segregation of populations in Europe by age (latitudinal gradient), adults from various continental locations may mate assortatively in the Sargasso Sea and may be able to maintain their integrity throughout the arrival waves (Maes and Volckaert 2002). Hence, the population in Europe may consist of an admixture of subpopulations. The development and maintenance of such a structure nevertheless requires temporal and/or spatial separation in the Sargasso Sea of spawning adult eels originating from different locations in Europe. This has to be followed by a non-random return of larvae to their parents' freshwater habitat through active swimming, seasonal changes in hydrodynamics or different pathways of the Gulf Stream (Wirth and Bernatchez 2001; Maes and Volckaert 2002). Dannewitz et al. (2005), however, provided evidence in favour of panmixia (no stable, isolation-by-distance (IBD)), indicating that any geographical component visible in a specific year would be inevitably lost due to the environmental dependency of age at maturity and the subsequent extensive mixing of formerly distinct spawning cohorts.

(b) The different life history of males and females also leads to different maturation patterns and timing. Males tend to mature at a size of around 40 cm and at an age of 3–4 years, while females mature at a size of >60 cm and at an age of 6–8 years (or older). Such maturation pattern complicates the potential to build up and maintain a stable genetic structure, because of the latitudinal bias in sex ratio (Tesch 2003). Although different ages at maturity between sexes do not constitute a restriction to develop and maintain population structure, a lack of geographical differentiation in favour of temporal differences may break up any temporal differentiation between cohorts distributed ''randomly'' over the European continent. Studies using mitochondrial DNA (mtDNA), which is inherited only maternally, did not show any geographical clustering (Avise et al. 1986; Sang et al. 1994; Lintas et al. 1998), pointing to the lack of power of this marker at the temporal scale studied or an unusual pattern of female mediated gene flow. The first hypothesis seems most plausible and could be indicative for a recent post-Pleistocene divergence pattern. A more thorough analysis of mtDNA markers on many individuals would probably be needed to fully assess the potential of this marker, as subtle

differences in marine species are more expected to occur at the haplotype frequency (quantitative) level than the haplotype distribution (qualitative) level.

(c) Adult eels exhibit differential migration departure times during spawning season, not only between populations in a North-South gradient but also between the sexes. For the smaller males it takes a longer time period to cover the distance of 6,000-km to the Sargasso Sea. Assuming a swimming speed of 0.5 body-lengths per second, a 80 cm female would reach the Sargasso Sea in 174 days, while this would take for a 50 cm male 278 days. Males usually depart 1–2 months earlier than females (Usui 1991; Tesch 2003). In the Netherlands, the seaward migration of silver males starts in August while the first females start migrating in September or October (Usui 1991). This protracted spawning period will increase the chance for overlap between possibly differentiated populations, although if spawning migration departure is genetically determined, cohort differentiation may be maintained throughout the spawning season. Nevertheless, the differential departure time over a latitudinal gradient and between sexes likely evolved to maximise the chance of group spawning in the Sargasso Sea at the most favourable period (coinciding with the larval bloom).

(d) The European eel exhibits the largest ''migration'' loop of all Anguillids (Tsukamoto et al. 2002). The potential breeding area is 5.2×10^6 km^2, so there can be a great deal of separation in space and time among spawning stocks. As long as the question has not been answered why the Sargasso Sea is so unique for eels reproduction, and as long as the exact location has not been confirmed, the total area can be seen as potential breeding grounds. From behavioural observations of spawning eels in aquaria (see Section ''Spawing behaviour and reproduction''), indication of collective and simultaneous spawning have been found; pheromones may play an important role in finding partners (McCleave 1987) (Section ''Maturation of European eel by environmental factors''). Hypothetically, adults from various continental locations could mate assortatively in sub-areas of the overall breeding grounds attracted to each other by specific odour. This separation mechanism may lead to a genetic mosaic consisting of isolated populations, although the temporal persistence of this mechanism remains questionable (Dannewitz et al. 2005; Maes 2005).

(e) The possibility to detect separate discrete spawning adults in the Sargasso Sea can be blurred due to the subsequent mixing of offspring during their journey to Europe. Random larval dispersal to the continent may mask active mechanisms of genetic structuring. In eels, however, active migration has been shown to distribute larvae along a latitudinal gradient following age/length (Lecomte-Finiger, 1994; Arai et al. 2000). Additionally, both North-Atlantic eel species show a strong directional migration to each continent, supporting the potential for active orientation of leptocephali larvae. Further indications for non-random larval dispersal are the observation of hybrids between American and European eels in Icelandic eel populations. Hybrids between both species, which are found almost exclusively in Iceland, may exhibit a genetically defined intermediate migrational behaviour (Avise et al. 1990; Maes 2005), with an intermediate developmental time. If randomly distributed across Europe, hybrids would have to be found in the Western British Isles, first passed by North-Atlantic currents.

(f) Finally, due to the unpredictability of the oceanic environment, marine species often show a very high variance in reproductive success and will evolve a strategy to maximise their offspring's survival (Hedgecock 1994). In eels, considering their extremely long trans-oceanic migration as adult and larvae, a protracted spawning period and random mating may be the best strategy to maximise the chance of reproducing in favourable conditions. Although seasonal reproduction of subpopulations could occur,

the chance of complete reproductive failure of certain groups is real (mismatch with algae bloom), endangering the survival of the species in the long term (Hedgecock 1994; Maes 2005; Pujolar et al. 2005b).

Future genetic research perspectives in the European eel

Conclusions drawn from molecular studies are a crucial tool to infer the panmictic status in the European eel. Considering the contrasting outcomes from recent molecular studies (Wirth and Bernatchez 2001 versus Dannewitz et al. 2005; Fig. 4), future research could focus on several of the following directions, to help clarify European eels evolution:

- The standardised small-scale analysis of recruiting juveniles may provide additional answers about the spatio-temporal partitioning of genetic variation and the presence/absence of a genetically determined spawning time (Pujolar et al. 2005b).
- The analysis of long—term time series of historical material may increase the confidence of genetic estimation of genetic population sizes. A first step would be the use of aged adults, so that back calculations till 30–40 years ago can be performed. More importantly, to assess the influence of heavy fisheries and yearly/decadal fluctuating oceanic conditions, the analysis of historical material covering the last century is urgently needed. This is now possible due to newly developed genetic techniques for ancient DNA and will enable the reliable calculation of a pre- and post-industrial fishery genetic population size. This knowledge is of crucial importance to preserve genetic variation, known to correlate with fitness components in eel (Maes et al. 2005; Pujolar et al. 2005a) and to define sound management issues.
- Although intraspecific genetic structure is very subtle in many eel species, neutral genetic variation might well underestimate adaptive variation over a broad environmental range. The development and study of novel markers under selection (such as Expressed Sequence Tags (ESTs) and Single Nucleotide Polymorphisms (SNPs) in candidate genes) would enable the detection of genetic variation underlying environmentally dependent fitness traits. SNPs are considered the markers of the future, due to their unambiguous scoring (compared to microsatellites), short fragment size (suitable for ancient DNA), neutral/adaptive characteristics and uniform polymorphism across the genome (Syvanen 2001).
- The current fishery pressure on the European eel stock is mostly due to the lack of artificial reproduction (but see Palstra et al. 2005 and references therein). For 30 years, researchers have been unable to produce economically profitable quantity of eels in aquaculture. Integrating additional oceanic knowledge into management strategies, together with the reduction of fisheries, might help define sustainable management issues, until artificial reproduction is successful.

The European eel has been studied for over hundred years and hypotheses concerning its population structure were tested using newly developed techniques every time they appeared. Nevertheless, the black box remains tightly closed for researchers. Many factors of its catadromous life-strategy increase the chance of panmixia, such as the variable age at maturity, the highly mixed spawning cohorts, the protracted spawning migration, the sex biased latitudinal distribution and the unpredictability of oceanic conditions. Nevertheless, several active components induce the chance for population divergence, such as assortative mating behaviour, the segregation of both North-Atlantic species in the Gulf Stream, active trans-oceanic larval migration, the presence of hybrids mainly in Iceland and the extremely large migration loop of the European eel compared to other species. In this review of traditional and genetic knowledge, it became clear that a geographical component, if existing, is almost invisible. On the other hand, genetic data supports strong temporal variation between and within years/cohorts possibly as a consequence of large variance in adult contribution and reproductive success (Dannewitz et al. 2005; Maes 2005; Pujolar

et al. 2005b). Oceanic forces are likely to represent one of the main actors in the observed temporal variation. The present climatic oscillations combined with the significance of oceanic forces in marine species prompts to the urgent assessment of temporal stability of the European eel stock, combining genetic, population dynamics and oceanic data. Only by tracking migrating adults and genetic monitoring their offspring through time, a reliable assessment of the factors influencing the population structure of the European eel will be possible.

Are European and American eels sharing the same spawning grounds?

There are only two species in the North-Atlantic Ocean, the European (*A. anguilla*) and the American eel (*A. rostrata*). Based on the number of vertebrae, the American eel (vertebrae ranging from 103 to 110, mean 107.1) can be distinguished from the European eel (vertebrae ranging from 110 to 119, mean 114.7) (Boëtius 1980). It is assumed that the spawning area of both eel species is located in the Sargasso Sea (Schmidt 1935; Ohno et al. 1973; Comparini and Rodino 1980; McCleave et al. 1987; Tesch and Wegner 1990). Several scenarios have been proposed for their origin, based on fossil records, plate tectonics, paleo-currents and a standard fish molecular clock. A first scenario is the dispersal of ancestral organisms through the Tethys Sea that separated 70 million years ago Laurasia (North-America and Eurasia) from Gondwana (South America, Australia, Africa and India). Along this sea, dispersal was possible through westerly paleocircumglobal equatorial currents (Aoyama and Tsukamoto 1997; Aoyama et al. 2001). Aoyama et al. (2001) suggest that *Anguilla* speciation started 43.5 Mya and that the North-Atlantic eels speciated some 10 Mya. Although such results were partially confirmed by another study (Bastrop et al. 2000), Lin et al. (2001), using a much larger fragment of the mitochondrial genome (cytochrome *b* and 12sRNA), proposed that the genus *Anguilla* speciated much more recently, some 20 Mya. This study hypothesised that the Atlantic eels colonised the North Atlantic through the Central American Isthmus (Panama) and speciated only some 3 Mya. Although these authors used a longer fragment and their speciation estimates are much more congruent with the accepted molecular clock, some incongruence remained. The absence of any eel species on the West coast of North-America or South America and the large phylogenetic distance with *A. japonica*, who should under this scenario be the ancestor of the North-Atlantic eels, suggest that the radiation events are much more complicated than expected using present day current and tectonic knowledge. A recent study analysing the complete mitochondrial genome gave additional support for the first hypothesis' dispersal route, but for the second hypothesis' speciation time (Minegishi et al. 2005). Speciation started 20 MyA and formed two main clades, the Atlantic-Oceanian group and the Indo-Pacific group. The present day geographical distribution does not seem to follow phylogenetic relationships anymore in the former, but does so in the latter group (Minegishi et al. 2005). Nuclear data might be the next step to clarify these ambiguities. These results also confirm the instability of morphological characters to discriminate the evolutionary relationships between *Anguilla* species, even after a thorough revision (Ege 1939; Watanabe et al. 2004a, b).

The divergence between both North-Atlantic species has been under discussion for decades. Tucker (1959) claimed that differentiating meristic characters (number of vertebrae) were under ecophenotypic selection during the transoceanic migration. The European eel would be the offspring of the American eel. Tucker (1959) suggested that the European eels do not participate in reproduction, because the distance to the Sargasso Sea was considered too far. Later work, based on variation at hemoglobin, transferrins and allozymes, however, confirmed the two species status (Fine et al. 1967; Drilhon et al. 1966, 1967; Drilhon and Fine 1968, de Ligny and Pantelouris 1973; Comparini and Rodino 1980; Comparini and Scoth 1982). Also two studies using specific proteins from respectively muscle and eye lens tissue indicated that the two Atlantic eel species have diverged far enough to have accumulated distinctive genes. One study was based on

electrofocusing methods using polyacrylamide gels for muscle protein differences (Jamieson and Turner 1980). Another study used eye lens proteins as genetic markers using patterns of isoelectric point variation (Jamieson and Teixeira 1991).

The allozyme locus *MDH-2** exhibits a nearly fixed difference between both species, although Williams and Koehn (1984) questioned the taxonomic reliability based on only one enzymatic locus. A mitochondrial DNA RFLP study showed conclusive results, separating both species with high confidence at 11 out of 14 restriction endonucleases, although the two North-Atlantic species exhibited the lowest genetic distance reported between *Anguilla* species (Avise et al. 1986; Tagliavini et al. 1995; Aoyama and Tsukamoto 1997; Ishikawa et al. 2004). The two Atlantic eel species cannot unambiguously be discriminated based on cytogenetic criteria like CMA3 staining, and FISH (fluroresence in situ hybridisation (Salvadori et al. 1995)), or C-and G-banding (Salvadori et al. 1996). Another study assessed the North-Atlantic eel speciation process using jointly distributed parasites (Marcogliese and Cone 1993). They reviewed the ''oceanic'' and the ''vicariance'' hypothesis of Avise et al. (1990), suggesting that the two species diverged either in sympatry through differential currents or through the influence of the ice sheets during the Pleistocene, respectively. In the first hypothesis, eels were supposed to live along a single coast (American or European) and disperse through changing currents to the opposite side of the Atlantic, with subsequent assortative mating. The second hypothesis states that the ancestor species had a broad continuous distribution, but split into two groups distributed at each side of the Atlantic under the influence of southward Pleistocene glaciations. The vicariance hypothesis seems to be the most likely to explain the present disjunct transcontinental distribution of the parasites in the study, which can only be transmitted horizontally by continental resident individuals living in freshwater (Marcogliese and Cone 1993). Probably, distinct dispersal patterns during spawning and/or unique spawning grounds provide the basis for the current split between the two species. It is also possible that there is a clear, genetically determined active choice of water currents by the larvae that ultimately brings them to their appropriate continent at different sides of the Atlantic (Kleckner and McCleave 1985). Another possibility is a strict genetically determined period of metamorphosis (Power and McCleave 1983; McCleave 1993; Cheng and Tzeng 1996), which ultimately brings the larvae into currents directing them to the American or European continent. The North-Atlantic eels have been found to be almost completely reproductively isolated, with a small fraction of genetic exchange. Iceland is mainly colonised by European eels, although a small proportion of eels exhibit a vertebrae number smaller than 110 (Avise et al. 1990).

Even though reproductive isolation is strong, indications for hybrids between European and American eel were detected in two studies. Williams and Koehn (1984) compared the *MDH-2** genotypes with the number of vertebrae and concluded that there must be a significant amount of gene flow between both species. Avise et al. (1990) evaluated mitochondrial DNA in addition to nuclear and meristic markers in Icelandic individuals. The data reflected cytonuclear disequilibria, most likely due to ongoing gene flow between both species. The study allowed the detection of pure individuals of both species besides hybrids and a quantification of the American eel material in Iceland (2–4%). Recently, Mank and Avise (2003) reassessed these conclusions with highly polymorphic microsatellites markers. Despite the high resolution and power expected from microsatellite markers (Manel et al. 2002; Anderson and Thompson 2002), surprisingly no indications for hybridisation were detected (Mank and Avise 2003). Most likely homoplasy was the main reason for the lack of discriminative power between both eel species. This result prompts for further investigations on the paradigm of complete isolation of European and American eels and reopens the debate of the existence and maintenance of a hybrid zone at more than 6,000 km from the spawning site.

Swimming capacity of silver eels

It has long been questioned whether fasting eels have sufficient energy reserves to cover the distance of 5,500 km travelling from the European coasts to the Sargasso Sea. Tucker (1959) had severe doubts whether the European eel would be able to swim across the ocean and suggested that all European eels are the offspring of American eels. Tucker's 'new solution to the Atlantic eel problem' provoked a long debate (D'Ancona and Tucker 1959; Deelder and Tucker 1960), but was finally rejected because a distinction could be made between the two Atlantic eel species based on genetic data (see section ''Are European and American eels sharing the same spawning grounds''). The theory of Tucker (1959), that the European eel is energetically unable to swim 6,000 km and would die in the continental waters, can also be rejected by the recent results of energy-balance studies performed in swim-tunnels. Those tunnels were specially developed for long distance migration studies with silver eels at our laboratories. The flow pattern of the tunnels has been evaluated using the Laser-Doppler method (van den Thillart et al. 2004). The oxygen consumption rate was calculated from the oxygen decline after closing the water-inlet with a magnetic valve. This was done daily during a swim period of several months at a fixed time (14.00–17.00 h PM), and oxygen level was recorded minutely on a data-acquisition system. We calculated oxygen consumption from the decline of the oxygen tension (van den Thillart et al. 2004, van Ginneken et al. 2005c). Results from this study were unexpected. Eels are extremely efficient swimmers due to their elongated flexible body, which is the basis for the characteristic eel-like (*anguilliform*) mode of locomotion. In one study, nine yellow eels were used with a body weight of 915 ± 58.4 g and a length of 74.7 ± 3.4 swimming 0.5 body-length per second at 19°C. The animals swam 117 days without feeding or resting, day and night. During this period the eels succeeded in covering a distance of 5533 ± 354 km (Fig. 5). The loss of weight for the swimming animals over the period of 117 days was approximately 180.3 ± 38.2 g, which corresponds to 19.7% of the initial total body weight. By two independent methods, oxygen consumption, and carcass composition, we calculated the energy consumed over a six-month swimming period, which we expressed in the COT (gross energy costs of transportation) value. This is the total amount of energy (kJ) it takes to transport one-kilogram body weight over 1-km at a given speed (Schmidt-Nielsen 1972). Data from the literature for several

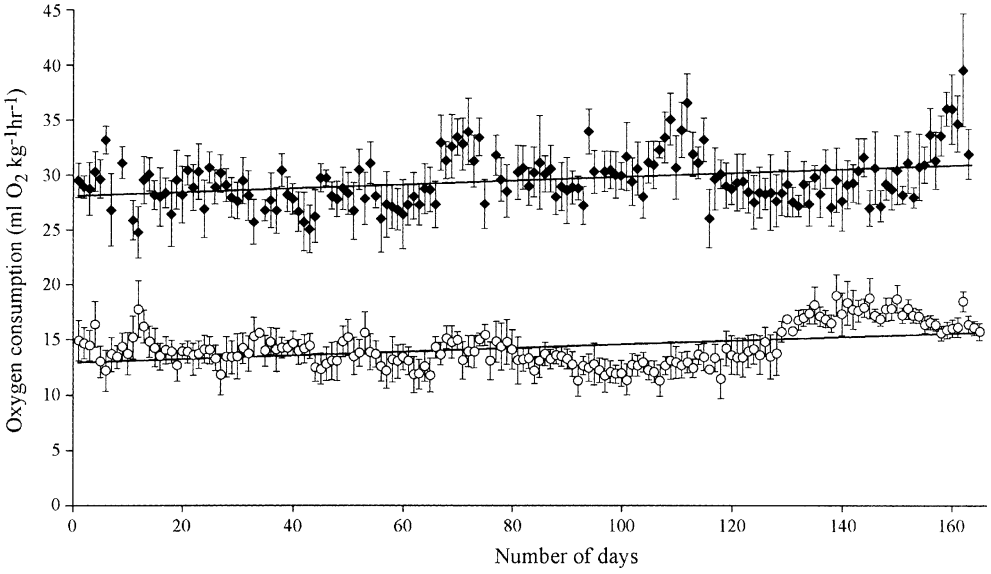

Fig. 5 Oxygen consumption of fasting yellow eels from a hatchery (860 ± 81.9 g, 73.1 ± 3.8 cm) during a 6 months period of rest or 6 months of continuously swimming at 0.5 BL/s at 19°C. Regression lines: Rest-group: Y=0.0326 X+25.294; Swim-group: Y=0.0394X+54.86. Diamonds: (swimming), circles (resting). (van Ginneken et al. 2005c)

sub-carangiform adult fish species, such as salmon, gave COT values in the range of 2.52–2.58 kJ/kg/km (Brett 1973). The oxygen consumption data and carcass analyses gave both COT values of 0.42 and 0.62, respectively. This means that eel swim four to six times more efficiently than non-anguilliform fish such as trout and salmon (van Ginneken et al. 2005d). Analysis of body constituents of the eels at the start and at the end of the experiment revealed that the ratio of all three substrates (lipid, carbohydrate, and protein) remained constant despite significant weight losses. This means that body composition did not change during the 6 months and that fat, protein, and carbohydrate were used in the same proportion (van Ginneken et al. 2005c).

To confirm this difference in swimming efficiency, we allowed eels and trout of the same body weight to swim in our swim tunnels at 18° ± 0.3°C at comparable body speed in our experimental set up for 1 week. European eels (n=5, 155.0 ± 18.3 g, 43.2 ± 3.2 cm) and rainbow trout (*Oncorhynchus mykiss*, n=5, 161.5 ± 21.5 g, 24.6 ± 1.0 cm were selected to swim in separate swim tunnels continuously at respectively 0.5 BL/s (21.5 ± 1.6 cm/s) and 0.7 BL/s (17.2 ± 0.7 cm/s). The eels and trout covered a mean distance of 132.5 ± 12.1 km and 102.8 ± 2.3 km respectively during 7 days of continuous swimming. Oxygen consumption rates allows us to calculate COT values of 0.68 (eel) and 2.73 (trout) kJ/kg/km. Video films of swimming animals ensured us that the fish were swimming freely and did not benefit from wall effects. This experiment provided two important results: first, the COT value of the small eels is close to that of the larger eels used in the 5,500-km experiment. Second, the observed COT value of the trout in this study is close to previously published values for salmonids (Brett 1973). Hence, we concluded that eels swim around four times more efficiently than salmonids (van Ginneken et al. 2005d).

An explanation for this phenomenon may lie in the swimming behaviour and muscle activity patterns of eels, as described by Gillis (1998). At low swimming speed eels do not use anterior muscle, only those located more posteriorly. Thus eels need to recruit only a small percentage of the swimming musculature to swim speeds of 0.5 BL/s. That eels swim at relatively low swimming speed comes from several animal tracking studies under natural conditions. High speed is not characteristic of the pure anguilliform mode, most reports mention speeds around 0.5–1 BL/s. For example American eels equipped with pressure sensing ultrasonic transmitters made frequent dives from the surface to the bottom during hours of daylight and darkness at speeds of 0.8–1.1 BL/s. The maximum rate of ascent was 0.6–0.8 BL/s (Stasko and Rommel 1974). Migrating Japanese silver eels (*Anguilla japonica*) have been tracked in the open ocean at a mean speed of 0.48 BL/s (Aoyama et al. 1999).

In a study with yellow- and silver-phase European eels fitted with 300 kHz transponding acoustic tags and tracked by sector-scanning sonar in the western North Sea for 58 h their modest mean swimming speed in midwater was 0.45–0.75 BL/s (McCleave and Arnold 1999). So all these studies indicate that the swimming speed of migrating yellow and silver eels is between 0.5–1 BL/s.

Some eels used selective tidal stream transport to move northward. (McCleave and Arnold 1999). At this moment we can speculate about the migration of silver eels. Probably they use selective tidal stream transport to cross the continental shelf wherever there are fast and directional tidal streams. Tides also exist in the ocean, so there is a possibility that they also get an assisted passage across the Atlantic if they travel close to the seabed. Otherwise, of course, they may follow prevailing surface currents to get back to the Sargasso. (Personal communication Dr. Geoff Arnold). It would be a challenge to get this information in future studies using archival tags (see Section ''Tracking silver eel migrations'').

An additional advantage for migrating eels under natural conditions, sometimes at depths of 2,000 m (Robins et al. 1979), is the improved efficiency of their oxidative phosphorylation at high pressure (Theron et al. 2000).

Although we can speculate about the mechanism which explains the efficiency of *anguilliform* movement, in future studies, hydrodynamics has to explain how does undulatory swimming work. Therefore two main questions have to be addressed: (a) the topic of the muscle design: which

muscle arrangement best suits the task of bending the body, (b) how does the fish convert muscle power into swimming power (personal communication: Dr.Ulrike Muller, Wageningen University, The Netherlands).

COT values from our study (van Ginneken et al. 2005c) confirm our earlier observation about the swimming capacity of eels suggesting that starving eels are, due to the low energy costs of transport, able to cover long distances (van Ginneken and van den Thillart 2000). In this recent study, we demonstrated that silver eels could swim at very low energy consumption levels, which enables them to use only 40% of their fat stores for crossing the Atlantic. The remaining 60% of the fat stores are sufficient for gonad development, in theory reaching a GSI of 22 (van Ginneken and van den Thillart 2000). This low energy cost for migration of eels is probably the basis for its uncommon catadromic life cycle with exceptional migratory patterns to their spawning grounds several thousand kilometres away: the European eel travels over 5,500 km to the Sargasso Sea (Schmidt 1923; McCleave and Kleckner 1987; Tesch 1982; Tesch and Wegner 1990); the American eel migrates over 4,000 km also to the Sargasso Sea (Castonguay and McCleave 1987; McCleave and Kleckner 1987; Tesch and Wegner 1990); the Australian eel (*A. australis*) travels over 5,000 km into the Pacific Ocean to spawn (Jellyman 1987); and the Japanese eel (*A. japonica*) travels over 4,000 km to the Marianna Islands in the Philippines to spawn (Tsukamoto 1992).

It can be opposed to the 5,500 km swim study (van Ginneken et al. 2005c) that hatchery eels have an extremely good nutritional condition and the same may not be true for the wild population (Svedäng and Wickström 1997). Therefore, the swimming ability of eels presented in our recent study can not exclude the possibility that recent declines in wild European eel populations may be due to (e.g.) diminished natural food supplies. Also other factors like parasites (Haenen 1995), pollution, viruses (van Ginneken et al. 2004, 2005a) and restocking programs with weak slow growing animals from aquaculture can ultimately have its impact on the quality of the standing population.

Migration and spawning depth

There is only one published study looking at eel migration at great depth where a migrating eel with a swollen belly was photographed in the waters off the Bahamas at 2000 m depth (Robins et al. 1979). Changes in body characteristics like enlargement of the eyes (Pankhurst 1982; Pankhurst and Lythgoe 1983) and the silvering of the body during metamorphosis from yellow towards the silver stage (Tesch 2003) have been documented as physiological and morphological adaptations to a new life phase in the oceanic environment. The visual sensitivity of the retina pigments also changes from green-sensitive to blue-sensitive during metamorphosis of the European eel (Wood and Partridge 1993; Archer et al. 1995).

Interestingly, indirect evidence suggests that migratory adults are adapted endocrinologically and physiologically for swimming and spawning within the upper 500 hundred meters, the epi- and upper meso-pelagic zones. Endocrinological evidence came from a field study by Dufour and Fontaine (1985) where cages with silver eels were sunken in the Mediterranean Sea at a depth of 450 m. Positive results which are indicative for maturation were recorded; a slight increase in ovarian development (GSI of 1.56 in control group compared to a GSI of 2.18 in pressure exposed group) was observed while the pituitary gonadotropin content increased by a factor 27 compared to the control group. Physiological evidence came from the observations of eel swimbladders and their ability to maintain swimbladder volume at depth. It is hypothesised that migration and spawning occur in the pelagic zone of the upper two hundred meters (Kleckner 1980).

Swimming with a swollen belly due to gonad development might not be very energetically efficient from a hydrodynamic point of view. Therefore, during the first part of the migratory passage development of the gonad has to be delayed; swimming at depths with temperatures less than 10°C can postpone the maturation process. This assumption is based on the observation of artificial maturation experiments with hormonally treated eels showing that the development of the

gonad is temperature dependent. Full sexual maturation in male *Anguilla anguilla* takes about 20 days at 25°C and about 60 days at 15°C, but gonadal development does not progress at temperatures below 10°C (Boëtius and Boëtius 1967, 1980). During initial migration low temperatures may be selected while upon arrival at the spawning area, eels have access to warm surface layers that accelerate maturation in preparation for spawning.

There are several indications from fisheries harvest and telemetry studies, which provide direct evidence for eels swimming and spawning at relatively shallow depths. However, care has to be taken in the interpretation of these data because the number of eels caught or sampled is very low. Silver phase *A. anguilla* have been caught in the eastern North Atlantic by pelagic trawls towed at maximum depths of 325 m (Ernst 1977). A migrating maturing female eel has been caught at a depth of 500 m close to the Azores in a deep sea trench of 2000 m. This eel had a GSI of 10 and gonads containing oocytes at advanced stage 3 (Bast and Klinkhardt 1988). Silver eels have also been recovered from stomachs of bottom-dwelling fishes captured at depths of more than 700 m (Reinsch 1968).

Several telemetry studies gave information about depth and temperature preference in eels. Again care has to be taken in interpreting these data because the number of studies and animals is low. A second point of concern is the extrapolation of results from telemetry studies in relatively shallow coastal waters to the deep ocean. Silver eels, which were tracked when they left the continental slope off the Bay of Biscay and west of Spain, occupied depths of at least 400 m, but selected shallower depths (50–215 m) at night (Tesch 1978). Studies in the western Mediterranean Sea tracking eels provided information on thermal preference. Eels tended to swim in the 13°C hypolimnion, but regularly crossed the thermocline during vertical migrations (especially at night) into surface waters as warm as 18°C. Preferred depth at night was 196 m and 344 m during daylight (Tesch 1989).

In a laboratory experiment, final preferred temperatures (FPT) of adult pre-migratory and migratory American eels were determined using chronic tests in a horizontal thermal gradient. The Final Preferred Temperature (FPT) is the temperature an animal ultimately selects in a horizontal thermal gradient after chronic exposure. Results indicated that both mature and non-developing *Anguilla rostrata* in saltwater had mean FPTs of 17.5°C, which is indicative of selection for a relatively high temperature (Haro 1991). Most observations from field studies indicate that migration of adult silver eels occurs in the upper 500 m of the open ocean and is a shallow-water phenomenon. There is a clear diurnal rhythm with eels occupying shallow, warm depths at night and diving to deeper, colder depths during the day to avoid high light intensities (Tesch 1989).

Information about the depth of spawning has been extrapolated from data on the release of hormone treated females tagged with transmitters, and on larvae catches. Again, the number of telemetry studies and the number of radio transmitter tagged animals is low. Releasing hormone treated mature female adults tagged with radio transmitters in the Sargasso Sea demonstrated a preference for the upper zone of the ocean at depths of 250–270 m and at temperature 18.7–18.8°C (Fricke and Kaese 1995). However, in the study of Tesch (1989) the maximum swimming depth of hormone treated silver female eels in the Sargasso Sea was nearly 700 m. Hormone treated female Japanese silver eels tagged with ultrasonic transmitters were released at their supposed spawning grounds in the western Pacific Ocean near sea-mounts on the West Mariana Ridge. These eels preferred relatively shallow water, swimming at a depth ranging from 81 to 172 m and at relatively high temperatures of 18–28°C (Aoyama et al. 1999). Interestingly, the catch of *Anguilla* larvae <5 mm confirmed these observations. The smallest (probably just hatched) larvae were found at depths between 50 and 300 m with temperatures of 18–24°C respectively (Castonguay and McCleave 1987). Those temperatures are close to the final preferred temperature (FPT) of sexually mature *Anguilla rostrata* (17.5°C), so spawning probably takes plays in the upper 200 m of the ocean at temperatures close to FPT (Haro 1991).

The spawning period

The major question regarding the timing of spawning is whether the putative spawning time derived from collections of small leptocephali is compatible with departure times and swimming estimates for silver eels. Usui (1991) reported that male European silver eels (approximately 40 cm) depart as early as August from the European coast to the Sargasso Sea, while female silver eels (mean body length ≥50 cm) depart 1 or 2 months later during September–October. It is possible that female eels arrive later in the coastal areas because they dominate low density up-river populations and thus have further to migrate downstream before reaching the sea. In contrast, males live in lower coastal areas and lagoons (Tesch 1977). Another explanation is that because of the males' smaller body length they have a lower cruising speed. Assuming a cruising speed of 1 BL/s, males would perform the 6000-km journey in 174 days, while females could perform the journey to the Sargasso Sea in only 139 days. The difference in migration time between males and females corresponds to approximately 1 month which could explain why males depart 1 month earlier. Ultimately males and females will meet each other in the Sargasso Sea to spawn as reported by Schmidt (1923) and the different publications produced by the group of McCleave and the group of Tesch (for references see Section ''The location of the spawning areas'').

Assuming a swimming speed between 0.5 and 1.0 body length per second they will reach the Sargasso Sea exactly 6 months later in the same period when recently hatched larvae have been observed: from March into June for the European eel and from February into April for the American eel (Kleckner et al. 1983; McCleave and Kleckner 1985; McCleave et al. 1987). So spawning of the European and American eel species is partially sympatric in space and time (McCleave et al. 1987) (see also Section ''The location of the spawning areas'').

The assumed swimming speed of 0.5–1.0 BL/s for endurance performance of eels was based on two types of laboratory experiments. Measurements of stress hormones, substrates, the ionic balance and lactic acid with groups of eels at different swimming velocities up to 3 BL/s. From these experiments we conclude that a relatively low cruising speed of up to 2 BL/s for eels could be characteristic for this catadromic long distance traveller (van Ginneken et al. 2002). The second type of experiment was based on oxygen consumption data which gave similar results (Palstra, Leiden University, The Netherlands, unpublished data).

Spawning behaviour and reproduction

Although the literature on hormone-induced reproduction in eel species is extensive (see reviews: Ohta et al.1997; Pederson 2003; van Ginneken et al. 2005d; Palstra et al. 2005), no clear descriptions are given of spawning behaviour of eels in the laboratory. Most aquaculture literature on this topic generally describe 'stripping procedures' to mix fertile eggs and sperm. The only report in literature that gives ethological data is a report by Boëtius and Boëtius (1980) which photographed a male eel in an aquarium releasing sperm with a mature swimming female with a swollen belly. In order to answer the question if spawning occurs at the surface, our laboratory made observations of spawning behaviour with hormone treated animals. Three types of spawning behaviour were documented during this experiment (van Ginneken et al. 2005d) female–female, male–female and male–male interactions (Fig. 6).

The two females (1.5–2 kg) that were used in this experiment hung lethargically for hours or cruised together (33.6% and 66.4% respectively) (van Ginneken et al. 2005d). Male–female interactions we observed showed sperm release by several males with one female.

In relative percentages, the different forms of spawning behaviour can be classified as follows: (a) approaching the head region of the female (57.7%); (b) touching the operculum (39.4%); (c) approaching the urogenital area (2.9%) by the males (total observation 725 s, Fig. 6). Non-sticky pelagic eggs were released to the surrounding water and the parents showed absence of parental care so their behaviour can be classified as non-guarding (van Ginneken et al. 2005d). Maximum

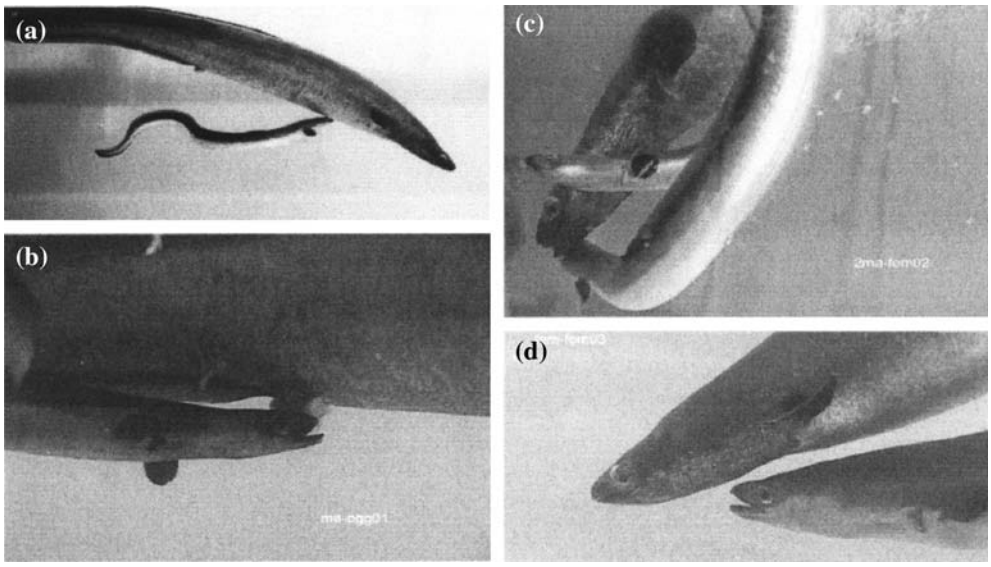

Fig. 6 Spawning behaviour of artificially matured European eel (*Anguilla anguilla* L.). Two females were used, together with successively 3 trios of males to record their spawning behaviour in the 4000-liter aquarium: (**a**) Male stimulates female at the head region, (**b**) Male attracted by the urogenital region of the female, (**c**) Mass spawning, several males with one female with release of sperm, (**d**) Interaction between females. Two females chasing each other. Induced spawning behaviour of eels was massive and simultaneous. (van Ginneken et al. 2005d)

speed of eggs rising to the surface in a water column was 2.24 ± 0.33 m/h.

Male–male interactions involved both males chasing each other seldomly releasing sperm. (van Ginneken et al. 2005d).

This study is an important observation documenting for the first time spawning behaviour in European eels. Based on these observations we concluded that induced spawning of European eel was collective and simultaneous possibly triggered by pheromones (van Ginneken et al. 2005d).

Maturation of European eel by environmental factors

One of the mysteries of the life cycle of the European eel is the endocrinological mechanisms which induce maturation of the gonads during their catadromous migration to the Sargasso Sea. When eels first migrate to the ocean in autumn, there is limited development of the gonad (GSI=1–2). If we keep these animals in aquarium boxes, there is no further development of the gonad; external environmental triggers for gonad maturation are lacking.

Dufour (1994) demonstrated, a prepubertal neuroendocrine blockage in the European eel at in the silver stage. Gonadotropin-releasing hormone (GnRH) in the pituitary is deficient in this blockage, and an inhibition by dopamine was found (Dufour 1994). Both factors are responsible for the lack of production of gonadotropin (GTH) by the pituitary and a blockage in the release of GTH resulting in immature gonads. This led to the hypothesis that sexual immaturity in silver eels is caused by a dual blockage situated in the hypothalamous-pituitary axis of the brain.

The endocrinological mechanism by which this dual blockage is reversed is not yet clear. Although no adult eel has ever been caught in the Sargasso Sea to determine GSI, observations of hormone treated animals showed that GSI values in mature animals may vary between 40 and 70 (references in van Ginneken et al. 2005d). Based on these observations, we conclude that maturation and development of the gonad is triggered by external environmental factors that the animals are exposed to during their 6,000-km migration to the Sargasso Sea. It is not yet known which environmental factors can induce a final maturation of the animals.

For the maturation of migrating silver eel several environmental stimuli have been suggested, including temperature (Boëtius and Boëtius 1967), light (Nilsson et al. 1981), salinity (Nilsson et al. 1981) and pressure (Fontaine 1993). The latter factor is based on one observation of a migrating eel with a swollen belly at the Bahamas at 2,000-m depth (Robins et al. 1979).

The first three environmental factors (temperature, light, and salinity) have been found to have no clear effect on the hypothalamo-pituitary-gonad axis in eels (Boëtius and Boëtius 1967; Nilsson et al. 1981). Water pressure has been investigated in the laboratory (Sebert and Barthelemy 1985, Simon et al. 1988), as well as in field studies (Dufour and Fontaine 1985). Laboratory studies with eels placed under pressure at 2.5 Mpa (Nilsson et al. 1981) and 101 atmospheres (Sebert and Barthelemy 1985; Simon et al. 1988), physiological changes were observed in the metabolism but not in maturation of the gonads. This was still the case after long term exposure to high-pressure of 1 month (Simon et al. 1988), or four months (Nilsson et al. 1981). Only one study has recorded a stimulation of the HPG-axis. In this field study (Dufour and Fontaine 1985), cages with silver eels were sunk in the Mediterranean Sea at a depths of 450 m. This resulted in a slight ovarian development; the authors reported a GSI of 1.56 in the control group compared to a GSI of 2.18 in the pressure exposed group. But the most remarkable change was the observation that the pituitary gonadotropin content increased by a factor 27 compared to the control group (Dufour and Fontaine 1985).

Remarkably, physical exercise has never previously been investigated as a potential stimulating factor. We hypothesise that maturation can be induced by exercise, because enormous physiological and endocrinological changes are the result of exercise in catadromous and anadromous fish species (Smith 1985). The Leiden group performed experiments to investigate the effect of long distance swimming on the HPG-axis and cortisol levels of European eel. Therefore, we studied the effects of swimming performance on maturation parameters in European eel (*Anguilla anguilla* L.) in large (127 l) Blazka swim-tunnels, (unpublished results). Three year old hatchery eels (71.4 ± 4.2 cm) with a mean weight of 792.0 ± 104.3 g were used in this study. One group of eels swam for 173 days at 0.5 BL/s and covered a distance of 5533 ± 354 km. One group was kept in static water for 173 days (Rest group). A control group was sampled at the start of the experiment in order to determine the initial stage of reproductive development. At the end of the swim trial, the maturation parameters 11-ketotestosterone, pituitary levels of LH and plasma levels of estradiol were higher (although not significantly) in the swim compared to the rest group. This observation can be explained by some animals responding and others not. In addition, no significant differences were observed in most measured morphometric and reproductive parameters, including eye-index, gonadosomatic index, hepatosomatic index, and plasma levels of vitellogenin, cortisol and melanophore-stimulating hormone (MSH). Also, pituitary levels of both MSH, and adrenocorticotropic hormone (ACTH) were unaffected. In contrast, the oocyte diameter was found to be significantly higher in the swim compared to the rest group. Based on these observations we conclude that a period of prolonged swimming might be a physiological stimulus necessary for the onset of maturation in the European eel (unpublished results).

Tracking silver eel migrations

To date no silver eels have been caught either on migration in the open ocean or in the Sargasso Sea. Schmidt's hypothesis that *Anguilla anguilla* spawns in the western North Atlantic thus rests on the distribution of newly hatched larvae in the Sargasso Sea, near the assumed centre of spawning (Tesch 1982; Schoth and Tesch 1982; Wippelhauser et al. 1985; Castonguay and McCleave 1987; McCleave and Kleckner 1987; Kleckner and McCleave 1988; Tesch and Wegner 1990). Conclusive evidence in favour of Schmidt's hypothesis could be obtained in several ways, if the appropriate methodology were available. The location of spawning grounds could be deduced from the distribution of adult fish, if it were possible to catch silver eels in spawning condition at sea. The Sargasso Sea is, however, about 5000 m deep and

limited fishing with mid-water trawls to a depth of 2000 m (Post and Tesch 1982) has so far only succeeded in catching adult eels of the genus *Serrivomer*. Another approach would be to delineate the distribution of newly spawned eggs, but first it would be necessary to develop a method of differentiating the eggs and early larvae of *A. anguilla* from those of other anguillid eels. Because this cannot be done using morphological characteristics, a molecular approach would be needed (Watanabe et al., 2004a, 2004b). A third option would be to track the movements of silver eels throughout their migration from European rivers back to the Sargasso Sea using electronic tags.

Small archival tags (e.g. Metcalfe and Arnold 1997; Arnold and Dewar 2001) are eminently suitable for tracking individual fish over periods of a year or more. Temperature and pressure sensors provide information about the vertical movements of the fish in relation to the thermal structure of the water column and horizontal movements can be reconstructed using light-based geolocation techniques (e.g. Hill 1994; Arnold and Dewar 2001; Ekstrom 2004; Stokesbury et al. 2004; Teo et al. 2004). However, although useful for small demersal fish such as plaice and cod (e.g. Metcalfe and Arnold 1997) and large pelagic fish such as bluefin tuna (e.g. Block et al. 2005), archival tags are of little or no use for species, such as eels, where recapture rates or low or non-existent. For these species, the only practical alternative is to use pop-up archival tags (Block et al. 1998) programmed to detach themselves from the fish on a specific date, float to the surface and transmit archived data by radio to Service Argos (e.g. Taillade 1992). This service, which is based on a series of polar orbiting satellites established by the National Oceanographic & Atmospheric Administration (NOAA) in the USA and operated by CLS in France (http://www.cls.fr), offers a commercial service for remote data retrieval with two frequencies (401.648 & 401.652 MHz) dedicated to animal telemetry.

Pop-up archival tags, which are currently made by two commercial companies (Microwave Telemetry, Columbia, Maryland; Wildlife Computers, Redland, Washington) in the USA, have been used successfully on various species of sharks (e.g. Sims et al. 2003; Boustany et al. 2002), as well as tuna (e.g. Lutcavage et al. 1999; Block et al. 2001, 2005) and billfish (Holland 2003). They consist of an archival tag with light, temperature & pressure sensors, a radio transmitter and a microprocessor, which controls the release mechanism, as well as data recording and processing. Electronic circuits, sensors and batteries are contained within a cylindrical case (approx. 110×20 mm) with a nose-cone at the front and a large polystyrene float (approx. 55 mm long×40 mm diameter) at the rear. The nose-cone contains the mechanical components of the electrolytic release mechanism. A quarter wave length radio antenna (216 mm long) protrudes from the end of the float. The tag is towed horizontally behind the fish, but floats vertically after it has been detached. Surface transmission time typically varies between 10 and 20 days.

Although some preliminary studies have been carried out in New Zealand with female longfinned eels (*Anguilla dieffenbachi*) of 7.6–11.4 kg weight (Jellyman and Tsukamoto 2002), it is not practical to use pop-up tags with European eels unless the size of the tags can be reduced substantially. Whilst miniaturisation of electronic circuits and sensors and a reduction in battery size would help considerably, the main challenge is to develop a smaller flotation mechanism that imposes less drag on the swimming fish, but at the same time allows more effective radio transmission. This may be possible by replacing the solid float with a device that inflates after the tag is detached and is capable of lifting the radio aerial clear of the water after the tag has reached the sea surface. Pressure resistance must be increased to allow tags to operate at depths beyond the current limit of 2000 m and research is also needed into tag attachment methods to avoid the problem of premature release that commonly occurs in bluefin tuna (e.g. Wilson et al. 2005) and a number of other species.

If these difficulties can be overcome, small pop-up archival tags could provide the key to discovering the routes that silver eels follow during their spawning migrations. Although existing light-based geolocation techniques (Hill 1994;

Arnold and Dewar 2001; Musyl et al. 2001; Ekstrom 2004; Stokesbury et al. 2004; Teo et al. 2004) are sufficient to describe overall patterns of oceanic movement, more accurate estimates of position may become possible by including a hydrophone to receive sonar signals transmitted by a buoy or a ship. One approach might be to record location each time the fish passes within a few kilometres of a ship or a buoy, whose position is determined by GPS and transmitted underwater via an encoded sonar signal (Gudbjornsson et al. 2004). Technology to do this in the open sea, in areas covered by regular research vessel surveys, has been developed by Star-Oddi (Reykjavik) and is under evaluation in one of Iceland's largest fjords (http://www.star-oddi.com). Another, and possibly more suitable technique, would be to use a miniature version of the RAFOS float system and determine position by triangulation, using a miniature processor in the tag to compare the reception times of signals from three or four moored transmitters (Lee et al. 2002). This system is currently under development.

Although we presented a recent update of the literature on the life cycle, evolution and reproduction of eels in this review, still some major questions remain to be answered:

1. Where are the exact spawning grounds for different eel species?
2. What is the environmental stimulus for reproduction and does it vary by species?
3. What are the critical habitat and environmental parameters needed for successful reproduction for the eel in the wild?
4. What are the causes of the decline in the eel population and their genetic consequences on the long term?

Generation after generation, scientists have dedicated their time and energy to study the catadromous European eel (*Anguilla anguilla* L.). Although a long way has been covered since Aristotle's theory of spontaneous generation in eels, the endless quest to unveil the fascinating life cycle of this mysterious creature will ultimately have to take us back to the Sargasso Sea, where everything started. For 3 million years this species succeeded in maintaining its characteristic life style with a remote spawning in the tropical North Atlantic Ocean and a juvenile foraging life phase till partial maturation in freshwater systems on the European continent. However, the last two decades eel populations declined dramatically by 90–99%, probably due to the synergy between human activities and oceanic fluctuations, bringing this species to the brink of extinction. Not much time remains to pinpoint the real causes of this decline and consequently to prevent the irreversible loss of this mysterious species.

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