European Eels: Dutch Fisheries, Culture and Eel Migration

Chapter · August 2014

DOI: 10.1007/978-4-431-54529-3_4

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The Netherlands is largely wetlands, so the country is classic habitat for the European eel (*Anguilla anguilla*), which was until relatively recently a common fish of the marine/brackish coastal area, found in rivers and wetlands. At high tide, half the country would be flooded were it not for the dikes and other water controls. Notably, many dikes, dams and sluices have been improved in the Netherlands during the past 100 years, to such an extent that migration of any fish became almost impossible. In 2008 the Netherlands had 4,671 pumping stations, 8,488 dams and 2,278 sluices, which given their advanced engineering, resulted in an almost complete barrier to fish migration (Fig. 4.1; Kroes et al. 2008).

A crucial part of the income of Dutch freshwater fishers was and still is derived from fishing for eels. Unsurprisingly, therefore, attempts were already being made 50 years ago to restock waters with glass eels to maintain a stable population in the Netherlands, at least until the price of glass eels burgeoned from the 1980s. Thereafter, the eel population declined rapidly all over Europe (Fig. 4.2; ICES 2009). The numbers of glass eels arriving at the coasts dropped dramatically throughout Europe, by about 90 % within 10 years, and since 2000, glass-eel arrivals have numbered <2 % of the number of arrivals during the 1960s. The decline in eel numbers started with a moderate decline in yellow eels some 5–10 years before a decline in glass eels was recorded, indicating that the downturn in the eel population in Europe was almost certainly not attributable to oceanographic changes, but was based on changes in coastal and wetland habitat. In this respect, it is remarkable that the same pattern was observed for American, Japanese and European eels over the same period, although this does not mean that the cause was necessarily the same for all three species. However, because the habitats of the three eel species are all within well-populated, urbanized areas, it is likely that a complex of factors related to urbanization impaired all three.

In the past, many fishing villages in the Netherlands, particularly those adjacent to IJssel Lake, such as Volendam, Spakenburg, Urk, Harlingen and Lemmer, relied heavily on eel fishing, but as the eel population declined in the 1980s, fishers either moved onto other fish species or stopped fishing altogether. Still, however, there is evidence in all those villages of a past and present interest in eels, for instance in the maintenance of old fishing boats (Zuiderzee Botters) mainly now for recreation (Fig. 4.3). In Volendam, there is also an old building called "De Visafslag," which was still in use some years ago as a place to auction eels caught in Lake IJssel (Fig. 4.4). Lake IJssel was formerly known as "Zuiderzee" (IJssel Sea), an inland water body for which plans to close its link with the sea already existed in 1819. Real efforts to close it, however, started in 1912, with the actual engineering only commencing in 1927 with the construction of a dike 30 km long and 90 m wide. The construction work was completed in 1932, and the lake is now the largest in the Netherlands, with a surface area of 1,100 km^2.

Eels in the Netherlands were traditionally processed in several ways, although the preferred one was smoking the catch from Lake IJssel; that catch consisted largely of small male eels (30–40 cm long and 80–150 g) which were available year-round. Now, however, the much smaller catch from the lake is exclusively female, because of the negligible influx of glass eels today, showing that the sex ratio is primarily determined by population density. The smaller male eels processed these days are derived exclusively from farms. Most of the Dutch eel catch is now processed by a few large companies, still mainly in the form of smoked product (Fig. 4.5). Eel smoking is, however, a national pastime, many people know how to do it, and there are still contests for the best smoked eels. Indeed, even with the species IUCN red-listed as endangered, sports fishers rarely return their catch of eels to the water, in contrast to what they do with other fish species. Instead, they take the fish home and fry or smoke them.

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K. Tsukamoto and M. Kuroki (eds.), *Eels and Humans*, Humanity and the Sea,
DOI 10.1007/978-4-431-54529-3_4,

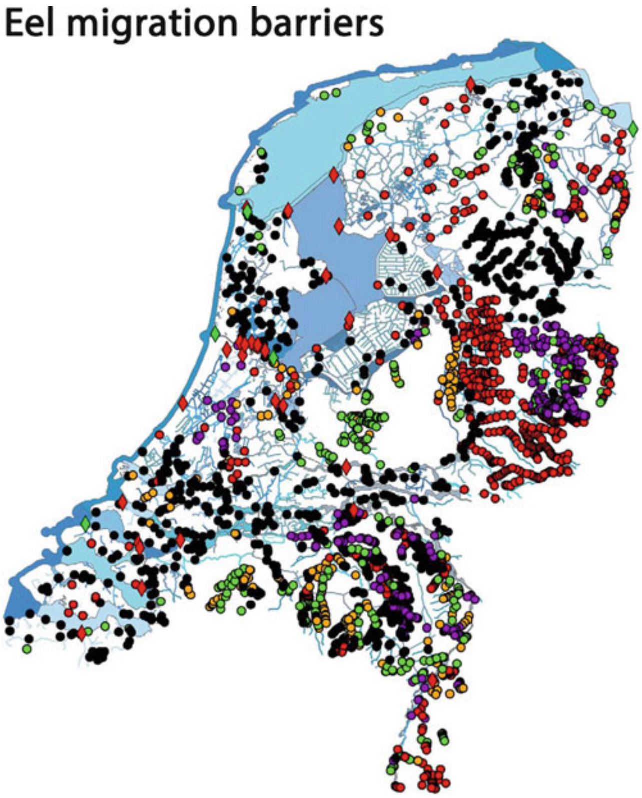

Fig. 4.1 The major barriers to eel migration in The Netherlands. The waterways are virtually closed to all fish migration by 4,671 pumping stations, 8,488 dams and 2,278 sluices (in 2008; modified from Ministry of Agriculture and Nature and Food Quality 2009). *Diamonds* depict barriers with (*green*) or without (*red*) a fish passage; *dots* depict critical sites with a passage in existence in 2008 (*green*), 2010 (*orange*), predicted by 2015 (*red*), predicted to be provided but date not yet known (*purple*), or with no passage currently planned (*black*)

Fig. 4.3 (**a**) Traditional fishing boats ("Zuiderzee Botters") still sail on IJssel Lake, but just for recreation. The boats are built for shallow water; they have side boards that are lowered when the winds are from the side to act as a keel. (**b**) Many of them are berthed in Spakenburg, an old Dutch eel-fishing village

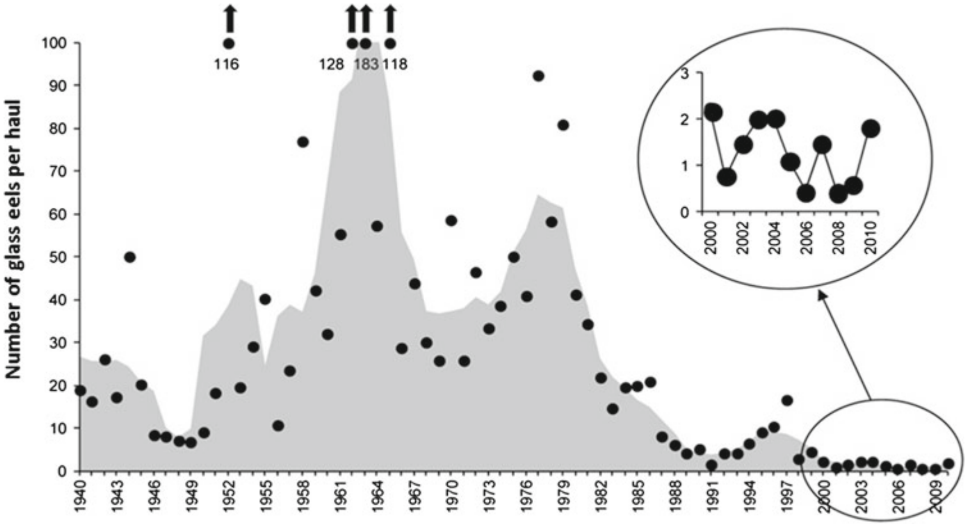

Fig. 4.2 Decline of the eel population in the Netherlands reflected in the results of glass-eel surveys, 1940–2010 (modified from de Graaf and Bierman 2010). The dots are the annual index, and the grey area the running 5-year means

Fig. 4.4 A “visafslag” in Volendam, a Dutch village well known for its eel fishing tradition. The old building was used exclusively to auction the fish brought in by the many IJssel Lake fishers. It was still in use up to a few years ago

Fig. 4.5 Eels in the Netherlands are mainly sold in smoked form, the favoured product. European eels have a high fat content, 20–30 %, which make them ideal for smoking

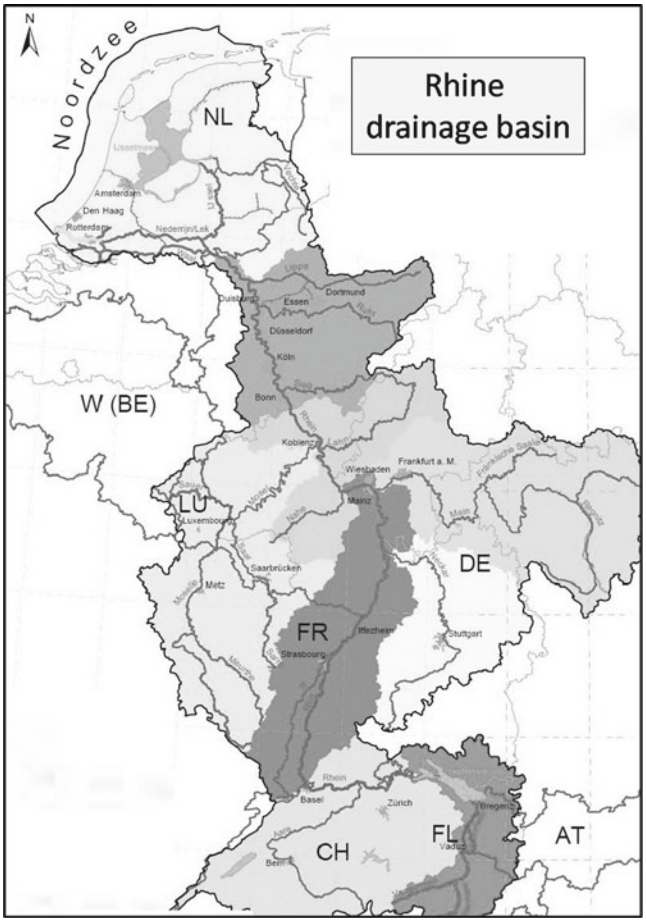

Fig. 4.6 The drainage basin of the Rhine, the largest river in Europe, which runs mainly through Switzerland (CH), Germany (DE), France (FR) and The Netherlands (NL), the last made up mainly of the river’s delta. Smaller rivers such as the Scheldt, Maas and Elbe also contribute to the delta and wetlands (modified from Ministry of Agriculture and Nature and Food Quality 2009). BE, Belgium; LU, Luxembourg; AT, Austria; IT, Italy

Although fykenets alone are deployed by commercial fishers, longlines and “peuren” (bobbing) are used occasionally by individual fishers in the wetlands. Longlines with a number of hooks are tied to a small stick placed in the grass in a ditch, where they are virtually impossible to detect. The tradition of “peuren” is a long-established means of fishing for eels, and it is still carried out by some as a sport; in Leiden there is an annual “peurbakken tocht,” a festival at which everyone shows up with their (well-decorated) boat. The bobbing technique relies on the typical bite response of eels, which do not let go of bait easily. For bait, rain worms are put on a line and bundled into a ball, connected to a weight on the line, and moved up and down with a stick just above the bottom. When an eel bites the bundle, it holds onto it tightly provided it is pulled carefully up in the water and into the boat.

History and Fishing Rights

The Netherlands span the delta of several rivers flowing into the sea along the west coast of Europe, the Rhine being the most important (Fig. 4.6). However, the wetlands were already well drained and the water level controlled by dams and sluices many hundreds of years ago, seawater and freshwater exchange taking place through sluices, and migratory fish such as eels readily passing the simple barriers, making sluice-fishing profitable. In fact, as long as 1,000 years ago, most eel fishing was associated with sluices. Indeed, in the Netherlands, eels have been historically far more important in inland waterways than salmon, and the fishing rights for eels were already well regulated and the exclusive right of feudal lords in the Middle Ages. The species was an important source of income to most of the counts of Holland (which is in the western part of the Netherlands), delivering as much as 20–40 % of their annual stipend (van Dam 1997).

The water level in the wetlands was generally controlled by monasteries that introduced drainage canals and sluices in order to encourage the people to remain living locally. However, the sluices then were not as effectively engineered as they are today, often leaking badly, allowing glass eels to enter and yellow and silver eels to exit with relative ease. As fishing rights had priority over water control, fishers often manipulated the sluices or even opened them to be able to catch more eels, impairing crop production and infuriating farmers and sometimes other citizens. Such almost open warfare between affected parties was at its worst in the fifteenth and sixteenth centuries (van Dam 1997). During the economic upturn then, a lot of peat was being dug in the wetlands to fuel the cities, resulting in serious land erosion and the formation of large lakes, which then also increased the habitat available for eels. The most successful sluice-fishing was carried out where the water drained into a river and/or the sea, and the most productive drainage point was at Haarlem, where water from Rijnland (the area between the cities of Amsterdam and Delft) drained into the Zuiderzee (now IJssel Lake). At sluices, fishers used all forms of fishing gear suitable for catching eels: fykenets, wicker pots, wicker fences and even trawls. Later, after 1500, polenet fishing was introduced, but that required investment beyond the means of many. Much of the trade in eels taking place at the end of the Middle Ages was in smoked and live product, and large quantities of live eels were transported in specially constructed barges to London, where Dutch traders sold their eels at the market (van Dam 1997).

Nowadays with tightly fitting sluice doors, high-frequency pumps and water flows irregularly directed into the wetlands, virtually no eels can enter or leave Dutch waterways and polders. In the past, the pumps were driven by windmills (Fig. 4.7a), with loosely fitting paddles transporting water over a small height difference, usually <1 m, which is no real barrier to an eel. Most lakes were shallow and often small, and they were the first to be drained using simple windmills. Having initially destroyed much of their land mining peat, the new technology using windmills allowed local populations to reclaim their lost land, and farmers around lakes started to form cooperatives. These organizations, referred to as "waterschappen" in Dutch, often constructed dikes and canals around their lake, then built one or two windmills to drain the main lake, referring to the reclaimed land as a "polder." Once the land had been reclaimed and a polder formed, the local cooperative was responsible for its maintenance, and waterschappen had already by the fifteenth century a status similar in officialdom to that of a city council. Such organizations still exist today, with the same responsibilities, each waterschap collecting taxes from its local inhabitants and using the income so derived exclusively for waterworks and water control. Waterschappen were the first experience of a democratic system in the Netherlands, the people living near the polder voting their representatives onto the council. Nowadays, though, some waterschappen have merged to increase their efficiency and supporting their ability to construct and maintain the large, complex engineering works required for modern society.

Fig. 4.7 (**a**) The Red Mill in Westlagelandspolder, now called the "Rode Polder," was built in 1632. It is close to Leiden (in the village of Oud Ade) in the area where the first lakes were drained using windmills. The upper part of the mill, the house, can be turned and positioned with beams on the outside to be aligned with the wind direction. (**b**) The "Cruquius" was the first steam-powered pumping station in the Netherlands and was one of the three steam-powered stations built to drain the last and largest lake in the Netherlands, the Haarlemmer Meer, which was for many years a threat to nearby cities

The largest lake in the Netherlands was Haarlemmer Lake, and relative to other lakes it was deep and large, at 18,000 ha. In fact, it was too large to be drained with windmills and was a threat to cities in the area, growing larger every year as a result of wave action during storms. Sometimes during those storms, the water destroyed the dikes, and almost every year a wide area was newly flooded. It was not until the nineteenth century, however, that an engineering solution became available with the design and construction of powerful steam-driven pumping stations at three locations around the lake. It then took 4 years to drain the lake, between 1848 and 1852. One of the steam-powered pumping stations, Cruquius, has been saved and is now a museum (Fig. 4.7b). The reclaimed land from Haarlemmer Lake was initially used for agriculture, but it now carries Amsterdam (Schiphol) airport, and the balance of the land is used to grow flowers and to accommodate high-tech industry and expanding towns.

Eel Fisheries, Management and Aquaculture

The European eel is in decline throughout its range and all current fisheries are considered outside sustainable limits. As mentioned elsewhere in this book, factors involved in the decline include overexploitation and other anthropogenic impacts (habitat loss, barriers to migration, pollution) plus natural impacts (predation, increasing parasite loads, climate change). Human-induced mortality is high on both juvenile (glass) and older (yellow and silver) eels, and eel recruitment throughout Europe is at a historical low and continuing to decline, with no obvious signs of recovery. Current levels of mortality induced by anthropogenic activity in the Netherlands and elsewhere are clearly unsustainable, so there is an urgent need for them to be reduced as low as possible until some recovery is recorded. Glass-eel recruitment data demonstrate a clear decline since the early 1980s, levels having dropped to between 1 and 9 % of the levels in the 1970s.

The paragraph above is based largely on a statement in the EIFAC/ICES working group on eels report of 2003 (ICES 2009), and the gravity of the situation regarding eels was soon noted by the European Commission, which in 2009 obliged Member States to implement an eel management plan for each water basin, to protect the eel population in Europe. The eel population throughout the continent decreased fast in the 1980s (Fig. 4.2), but because the real cause of the decline was not evident, it took a long time for mitigating action to be taken. Clearly, however, many factors played a role in the virtual collapse of the eel population, and it is probably the number of factors and indecision on which were the most important that made it difficult to decide on the action necessary to halt the decline and to attempt to stimulate recovery. One contributing factor has certainly been predation by cormorants, because such predation is known to have accounted for 30–50 % of the whole take of European eels during 1993/1994. Another contributing factor was the arrival in the early 1980s, likely with a shipment of Japanese eels (*Anguilla japonica*), of the eel swimbladder parasite *Anguillicola crassus*. That infestation spread fast in western Europe, probably because the European eel had no natural resistance to it. Indeed both the levels of infestation and the sizes of the parasite in European eels outstrip the levels recorded in Japanese eels. The parasite is clearly more destructive to the European eel than it is to the Japanese eel, because it not only impairs swimbladder function but also feeds on the blood of the host eel (Fig. 4.8). After repeated infections, the eel swimbladder becomes thick and ultimately constricts completely, such that it cannot be inflated by the gas gland, which has an obviously devastating effect on silver eels migrating to their spawning grounds across the Atlantic and conducting regular diurnal migrations. Without a functional swimbladder, the energy costs of swimming are very high (Palstra and van den Thillart 2010).

As stated above, the European Commission obliged its Member States to produce eel management plans with the aim of reducing mortality on the species and preserving the stock. With an estimated total production of eels in the Netherlands during 2009 of some 6,120 t (commercial fishing 920 t, sportfishing 200 t, aquaculture 5,000 t), the national plan implemented in that year is articulated in Ministry of Agriculture and Nature and Food Quality (2009). In summary, it stated that:

- there would be no fishing during the migratory season (September–November);
- 30 important barriers to migration would be removed;
- 600 fish passages would be created before 2015;
- a 35 % reduction in mortality at power plants would be sought;
- a restocking programme with glass eels would be established.

The objective of the plan was to ensure that 400–5,200 t of silver eels would be migrating annually into the North Sea from the Netherlands by the year 2090. The target is an escapement rate of silver eels of at least 40 % of the pristine situation, taken as that in 1970, and until that level was achieved, all fishing for eels in Europe is banned. In the Netherlands in 2010, all fishing for eels during their migration months (September, October and November) was stopped. To address the restocking target for glass eels, a group of eel fishers, eel farmers and members of the eel processing industry (in an organization referred to as “Future for Eel,” and subsequently as DUPAN) tried first to improve negative public sentiment about the threatened eel population because they were worried about both the reduced yield from the stock and the strict measures taken by Government. However, to make matters worse, Dutch supermarkets in 2010, influenced by NGOs such as WWF, Stichting Noordzee and Greenpeace, banned all products based on the European eel, and as a direct consequence of that decision, FFE/DUPAN started releasing silver eels into the North Sea (Fig. 4.9), arguing that attempting to restock with glass eels could not provide immediate help to the decimated eel population, because it took >12 years before surviving glass eels migrated as silver eels back to their spawning grounds. In the opinion of that group, therefore, releasing large female silver eels would be a more effective boost to the

Fig. 4.8 The swimbladder parasite *Anguillicola crassus*, a nematode that uses copepods and other fish as intermediate hosts. The larvae travel from the gut of the eel to the swimbladder, where they mature. Eggs leave the swimbladder for the gut via the pneumoduct. After repeat infections, the swimbladder wall thickens and cannot be inflated by the gas glands

Fig. 4.9 Large-scale release of silver eels into the North Sea by the "Future for Eel" foundation (FFE)

stock and might result in increased glass eel influx within as little as 2 years. The jury is still open on whether this effort will improve the situation!

Sports fishers, unlike commercial operators, rarely fish in open waters. Instead, they operate mainly from small boats or along the banks of canals, generally with rods. Commercial fishers use different techniques to catch eels, operating in rivers and open water mainly with fykenets, often with several connected to each other over a distance of several hundred metres and fixed with anchors (Fig. 4.10). Such gear is generally set along the side of the river, to preclude it being damaged by passing cargo ships. The modern boats used to catch eels differ greatly (Fig. 4.11) from traditional ones, but they still look impressive when operating in open water under a clear sky.

It was some 30 years ago that interest in eel aquaculture in the Netherlands burgeoned, and many pig farmers then

Fig. 4.10 Commercial eel fishers, fykenets and fishing boats. Fykenets are anchored and connected to each other along the river bank over a distance sometimes of >1 km

Fig. 4.11 Fishing boats in the Netherlands

Fig. 4.12 A modern eel farm with automatic feeders and water recirculation system. Eels can be held successfully at high density, but the major issues are to keep water flow rapid and water quality good (photo courtesy J. van Doren, reproduced with permission)

started their own eel production plant, using recirculation techniques and automatic feeding systems that allowed the plant to be run virtually automatically in confined spaces in small buildings (Fig. 4.12). Water recirculation has the advantages of limited heat loss, constant water condition and the ability to culture fish at high density, meaning of course less need for high-cost space and labour. Although profits have dropped because of the rising purchase price of glass eels, feed, water and electricity, these eel farms still produce more eels than the fishery. Eels at these farms are harvested after about 1–3 years when they have already grown to marketable size and when they tend to stop feeding and are about to adopt the silver phase. The farmers do not want their product to attain the silver phase, because it is more efficient economically for them to harvest the eels at the end of their main growing phase, so they then sell their product to processors, who mainly fillet and smoke it before any silvering takes place. Some eels are also sold whole smoked, the way the product was traditionally produced in the Netherlands (Fig. 4.13), but by far the largest part of eel production today is filleted smoked eel sold in sealed packaging. In the Netherlands, the smoking of eels is considered an art, so many smaller companies sell their product as “produced in the old-fashioned way.” However, bigger processors have the capacity to smoke large numbers of eels, so they import much of their product from elsewhere in Europe (Norway–Greece), using special trucks and holding the imported eels temporarily in an adjacent canal (Fig. 4.14). These bigger processors have a broad international network for import and export. Much of the product sold on is smoked, often in the old fashioned way, i.e. over smouldering wood chips that guarantee the exclusive flavour of Dutch smoked eel (Fig. 4.15).

Fig. 4.13 Smoked eels are sold whole and filleted, the latter becoming more popular as people become increasingly unwilling for their hands to be greasy after eating eels. Photos courtesy J. van Doren (*left*) and A. Koelewijn (*right*), reproduced with permission

Eel Migration–the Energy Requirements of Swimming

European eels have to cross the Atlantic Ocean twice: on their way to Europe they mainly drift passively in the Gulf Stream as leptocephalus larvae, arriving along the coast and entering the lower reaches of estuaries as glass eels and elvers, but when the survivors return as adults to the Sargasso Sea to spawn, they have to swim the ~6,000 km. Although the energy expenditure required for the massive return migration is enormous, the life history of the species does provide it with the ecological advantage of being able to be distributed over a wide area of coastal Europe, from Norway to Morocco and even into the Mediterranean Sea, as far afield as Greece and Egypt. This pattern of an outward passive drift of larvae with currents and an inward active spawning migration as adults is an innate characteristic of the species, because all 19 species of *Anguilla* (Minegishi et al. 2005) show it. However, only a few species migrate such great distances into the open ocean as the European eel *Anguilla anguilla*: these are *A. rostrata*, *A. japonica*, *A. australis*, *A. dieffenbachii* and *A. marmorata*. The shortest distance covered among these six species is that of *A. australis* and the longest that of *A. anguilla*, respectively ~2,000 and ~6,000 km.

Migrating eels do not feed, so they rely for their energy on fat stores which, when they leave freshwater, constitute as much as 30 % of body weight (Tesch 2003; van Ginneken et al. 2005; van den Thillart et al. 2007). European silver eels need to swim across the Atlantic Ocean within 6 months, because that is the difference in time between the date they leave the coast and the date the first larvae are observed in the Sargasso Sea. Therefore, minimum swimming speed would be 6,000 km in 6 months, or 0.4 m s^{-1}. To date, little is known about swimming speeds and the endurance of eels, and these parameters, plus the rate of oxygen consumption, are required for scientists to be able to answer questions about the energy requirements for eels to swim such long distances. Long-term swimming experiments require specialized equipment that needs to be able to run continuously for several months, and it is necessary too to be able to determine energy consumption at different swimming speeds, because there obviously needs to be sufficient energy left for the eels to be able to spawn when they eventually arrive at the position where they breed. From energy consumption values of other fish species, the energy stores of an eel (measured at 300 g of fat per kg of eel) would be depleted before 6,000 km of migrating without feeding. Hence, eels need to have an efficient means of swimming.

To study the swimming energetics of eels, 22 swim tunnels 2 m long were built and tested with female eels ~80 cm long (van den Thillart et al. 2004). The tunnels were tested for

Fig. 4.14 Live eels are imported to the Netherlands by truck and either kept in nets in a nearby canal or used immediately. A stunning technique, based on short electrical pulses, is now used to kill them humanely, and thereafter they are treated with salt to remove the slime before their gills and intestines are removed

Fig. 4.15 After cleaning, eels to be smoked are put on spikes and placed in large racks above smouldering woodchips that impart the traditional flavour. During the smoking process, much of the fat melts

homogeneity of water flow, calibrated with a laser–Doppler technique (van den Thillart et al. 2004). Extensive endurance swimming trials were carried out at Leiden University (van Ginneken and van den Thillart 2000; van Ginneken et al. 2005; Palstra et al. 2008; van den Thillart et al. 2009). The tunnels were of the Blazka type, consisting of two concentric tubes, with the inner tube and the outer ring having the same surface area, resulting in equal flow rates in the two compartments. A propeller pushes water into the outer ring and further into a bundle of flow streamers, to reduce the size of the vortices and generating a semi-lamellar flow (Fig. 4.16). Eels are obviously excellent swimmers, because placing them in flowing water is usually sufficient for most of them to start swimming actively. However, it is important in such experiments to preclude the fish from becoming stressed when being induced to swim; gradually altering the flow rate up and down gently during the first hour after experimental start-up is generally sufficient to stimulate them to swim. Once swimming, eels can swim for long periods at speeds of 0.4–0.8 body lengths (BL) s^{-1}. An endurance swimming trial has been performed with adult female eels swimming for 160 days at 0.5 BL s^{-1}, which would equate to a horizontal distance covered of 5,500 km. The energy consumption by such eels swimming continuously seems to be low, about 5 times less than that of salmonids (van Ginneken et al. 2005; van den Thillart et al. 2009), likely a selective force during evolution of the species. Despite male European eels being much smaller than females, 40 cm vs. 80 cm, they swim as well as females, and their energy costs of swimming appear to be even lower. Moreover, tested swimming in groups (Fig. 4.16c), the energy cost of swimming by males is even less, some 20–50 % less than when swimming alone (Burgerhout et al. 2013).

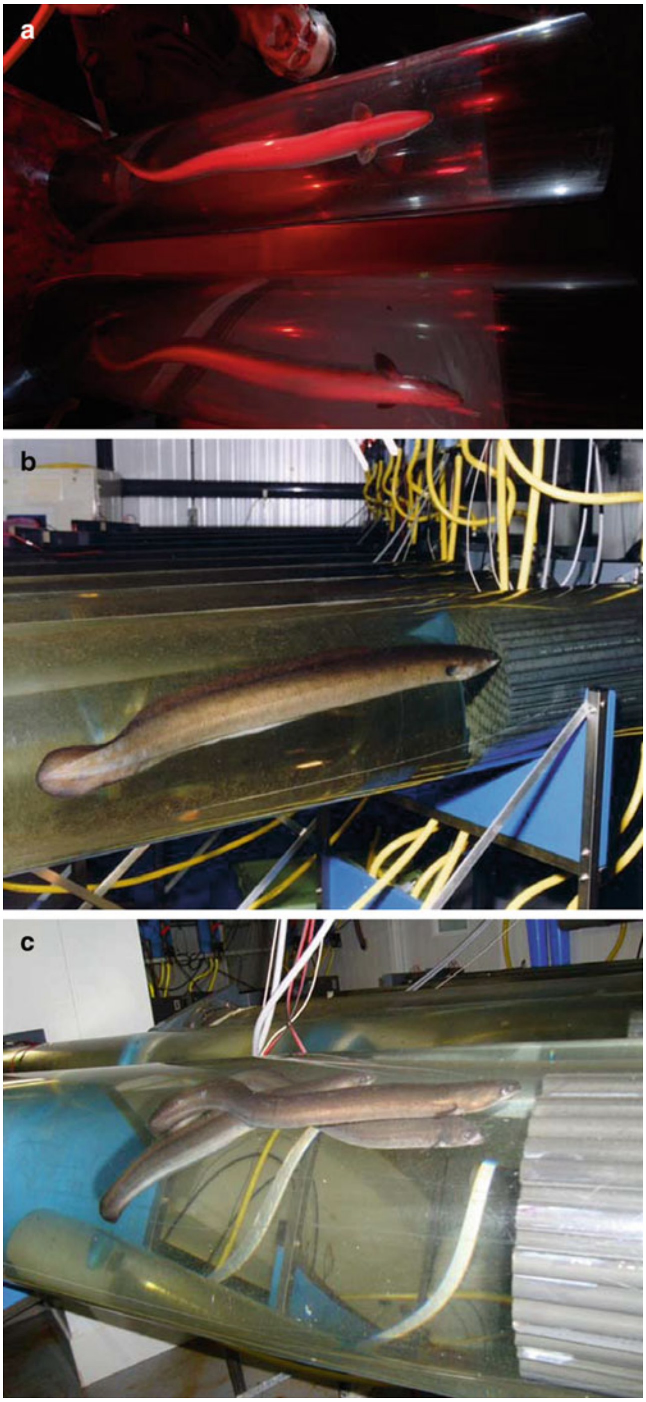

Fig. 4.16 Testing eel swimming stamina in a swimming tunnel consisting of two concentric perspex tubes 2 m long. (**a**) Eels in the tunnel, with red light used to limit stress–silver eels are virtually blind to red light (photo Doubilier, reproduced with permission). (**b**) Swimming tunnels are used to study long-distance migration. In the foreground is a tunnel with a 72-cm silver female eel. (**c**) Male eels, which are smaller than females, swimming in groups, which reduces energy expenditure (van den Thillart et al. 2004)

In experiments conducted in Leiden in swimming gutters, where it is possible to assess the swimming capacity of large groups, it has proven possible to study endurance swimming relative to sexual maturation. It is of note that silver eels leaving Europe in autumn are not yet mature, with a GSI (gonadosomatic index) of 1–2 %, and seldom >2 %. Therefore, the migrating eels must be maturing later, either during their migration across the Atlantic or perhaps when they arrive in the Sargasso Sea. One theory is that sustained swimming over a long period is a trigger that releases the inhibition against maturation exerted by certain brain centres. Results of experimentation to date do indicate that swimming is a trigger for maturation; males seemingly mature after swimming continuously for a few months and females show initial changes in the ovaries during the long swim. However, females clearly require an additional trigger to stimulate maturation. Knowledge of natural triggers is certainly important for future work on stimulating eels to spawn in captivity, because the repeated hormone injections upset the condition of the eel and are both expensive and time-consuming. Another way perhaps to improve eel reproduction under culture conditions would be to stimulate natural spawning behaviour (Fig. 4.17); mature males and females induce the final phases of maturation through pheromone signals. Natural maturation would probably be more effective than manual

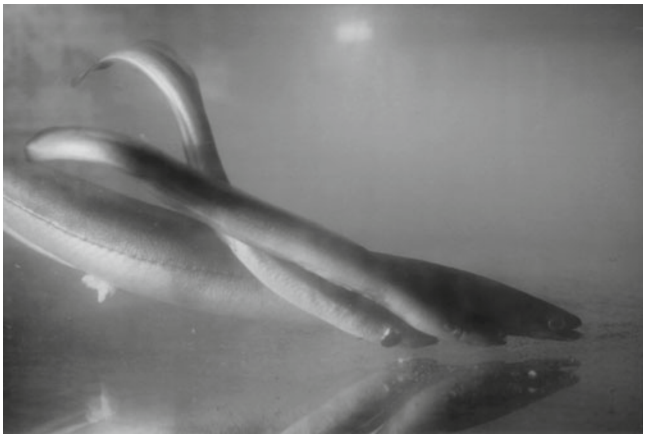

Fig. 4.17 The spawning behaviour of mature female and male silver eels. The female eels were treated with pituitary extract from carp and male eels with hCG (human Chorionic Gonadotropin) to induce final maturation (photo courtesy H. Berkhout, reproduced with permission)

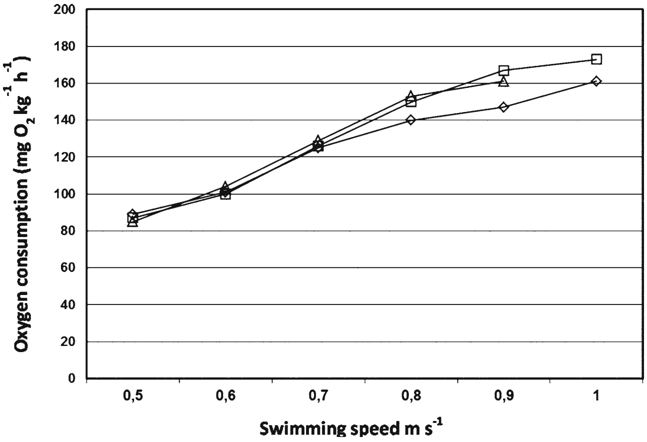

Fig. 4.18 The oxygen consumption of swimming eels. Energy consumption (mg O_2 kg^{-1} h^{-1}) increases almost linearly with swimming speed (m s^{-1}); with optimal (most efficient) speed calculated to be ~0.6 m s^{-1}. The energy cost of a 1 kg eel swimming at that speed is about five times less than that of a salmonid of similar size. In this particular experiment, 40 farmed female eels (0.9 ± 0.1 kg) were exposed to three swimming trials with stepwise increases of 0.1 m s^{-1} from 0.5 to 1.0 m s^{-1}. Tests 1 and 2 were at intervals of 2 h^{-1}. For the endurance test, which was conducted between tests 1 and 2, the eels swam 12 h day^{-1}, each consecutive day at a faster speed (modified after Palstra et al. 2008). Diamonds, test 1; triangles, endurance test; squares: test 2. Differences between the three tests were not significant

induction of maturation with injections of ovulation hormone such as DHP (17, 20-dihydroxy-4-pregnen-3-one).

To determine optimum swimming speed, experiments were carried out with eels swimming for extended periods at different swimming speeds (Palstra et al. 2008). Four groups of eels were tested in a swimming fitness protocol over a range of speeds of 0.5–1.0 m s^{-1}, corresponding to 0.6–1.2 BL s^{-1} (Fig. 4.18). In that study, eels were allowed to swim for 2 h at each speed from 0.5 to 1.0 m s^{-1} increasing in steps of 0.1 m s^{-1}. At each speed, oxygen consumption was measured continuously for 90 min and the maximum aerobic speed interpolated according to the method of Brett (1964). A group of 40 farmed eels was tested twice (tests 1 and 2) at 2-h intervals; each test took one day. In the week between tests 1 and 2 too, each eel was required to swim for 12 h day^{-1}, each day at a faster rate, i.e. 0.5, 0.6, 0.7, 0.8 and 0.9 m s^{-1}, to assess endurance. The rates of energy consumption were the same in the different tests, and it was concluded that, once eels start to swim, they do not alter their swimming mode, and more importantly, that the energy costs of swimming do not change. Eels are efficient swimmers, more so than many other species of fish, but when swimming they do not cope well with tags attached externally. Recently, PSATs (pop-up satellite tags), which have been used a few times to follow migrating eels (Jellyman and Tsukamoto 2002; Fig. 4.19), were tested in

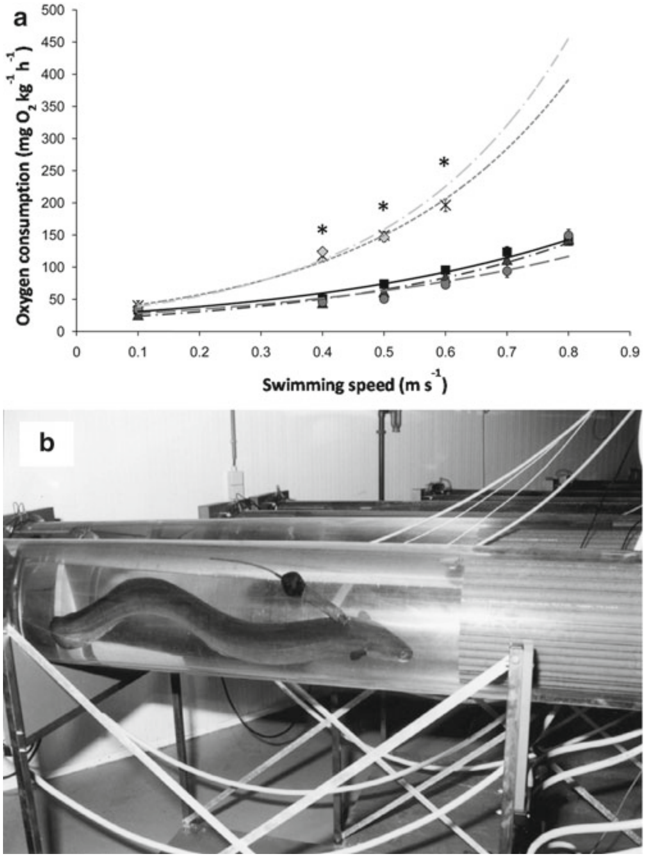

Fig. 4.19 An eel's swimming efficiency and endurance drop markedly when a tag is attached. (**a**) The rate of oxygen consumption (mg O_2 kg^{-1} h^{-1}) of European eels (~0.8 kg) swimming at 0.1, 0.4, 0.5, 0.6, 0.7 and 0.8 m s^{-1} with/without an attached pop-up satellite tag (PSAT), i.e. under five different conditions: no tag (*black squares*), after attachment of a base for the tag (*grey circles*), with tag attached (*grey diamonds*), with the same tag made neutrally buoyant (*crosses*), and after removal of the tag (*grey triangles*). The asterisks indicate significant differences ($p < 0.01$) between eels swimming with and without a tag. Eels carrying a tag could not swim faster than 0.6 m s^{-1}. The error bars (± s.e.) are indicated at each datapoint. Graph modified after Burgerhout et al. (2011). (**b**) A 1 kg European eel with a PSAT attached to it in the swimming tunnel

Fig. 4.20 The genomes of *Anguilla anguilla* and *A. japonica* were sequenced in January and July 2011, respectively, by ZFscreens BV, Leiden, Netherlands (http://www.zfscreens.com/home) in a consortium with K. Tsukamoto (Tokyo University), S. Dufour (MNHN, Paris), F-A. Weltzien (Oslo University), and the author

the Netherlands on eels swimming in a swimming tunnel (Burgerhout et al. 2011); the energy consumption with tags attached increased 2–3-fold. Moreover, the capacity to swim long distances decreased when tags were in place, as did peak swimming speed. Obviously, therefore, PSATs of their current size are not suitable for use in following eels right across the Atlantic.

Eels have always interested people because of the mystery surrounding them: for instance, what trigger makes them suddenly decide to migrate, exactly where do they spawn, how do the eels reach those spawning grounds, how deep can eels swim, how do eels reproduce, and how can eels be reproduced artificially. There are some new techniques that are helping to solve some of the mystery, and an important one is the sequencing of the eel genome and using that to monitor internal changes to the eel. With the genome of the European and Japanese eels now sequenced (Fig. 4.20), a major step forward has been taken, one that is crucial for the future of eel research (Henkel et al. 2012a, b).

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