Eels in Culture, Fisheries and Science in Denmark

3

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As in many other parts of the world, eels and their mysterious life cycle have always fascinated Danes. Almost everyone in Denmark, no matter their age, knows something about eels. In fact, the eel was once one of the country's most important food fish, and Denmark itself was one of the main European nations fishing it, partly because of the seasonal abundance of migrating silver eels leaving the Baltic Sea through the narrow Straits of Denmark. Eels were fished year-round even during winter (Fig. 3.1). Although the Danish eel fishery was carried out mainly by smallholders, eels were for many years traded extensively with other European countries. Today, though, fisheries for eels are limited by low abundance and consequently restrictive laws.

Denmark has a long tradition of research into the biology and ecology of the European eel (*Anguilla anguilla*). From the early 1900s, when Danish scientist Johannes Schmidt identified its spawning area in the Sargasso Sea, right up to today, scientists have actively researched eel migration and larval drift. Also, the laboratory studies on reproduction and spawning behaviour of eels by Inge and Jan Boëtius during the 1960s and 1970s raised interest in research on eel physiology and behaviour. Today, Danish research on the genetics, migration and captive reproduction of eels is widely respected.

Many aspects of eel biology still remain a mystery, however, so Danish research on European eels continues in a national as well as an international context. Some of the history and current knowledge is outlined briefly here, and we also discuss the long-standing relationship between humans and eels in Denmark, including looking at the significance of eels in Danish culture and society, e.g. in fisheries and as food.

Eel Biology

Like all species of freshwater eel (*Anguilla* sp.), the European eel is catadromous, i.e. they spawn in the sea and grow in freshwater or brackish habitats. Although spawning eels and their eggs have yet to be captured in the wild, the presence of newly hatched larvae in the Sargasso Sea in the western Atlantic reveals that to be the spawning area of the species. Those yolksac larvae develop into leaf-like, transparent leptocephalus larvae that drift with the ocean currents towards Europe and North Africa. On encountering the continental shelf, they transform into transparent glass eels, which have the characteristic eel shape and migrate actively into coastal waters; in Denmark, glass eels appear at the coast, usually from April to July. Then, while developing into pigmented elvers, they disperse into estuaries, fjords, river mouths, rivers and lakes and assume the form of yellow eels, characterised by a dark upper body and a yellowish abdomen. They feed on a variety of food, such as worms, caterpillars, grubs, shrimps, frogs, fish eggs, fry and small fish, their growth rate varying with temperature and food availability. In cold, fast-running streams, for instance, growth is slower than in shallow lakes, where the temperature can be high in summer. On average, eels in Denmark grow 2–5 cm year^{-1}. Sex is determined early in the yellow eel stage and sex ratios have been suggested to vary mainly

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Fig. 3.1 Winter eelers on the island of Lyø, Denmark, in the mid-1950s (photograph, Ole Højrup, © Thomas Højrup. In Fisherman and Boats on Roskilde Fiord: Past and Present by Rieck Flemming and Max Vinner, 1989. The Viking Ship Museum, Roskilde, Denmark)

as a result of differences in population density; in bays and lagoons where densities are high, males tend to dominate, whereas in areas of lower density, such as freshwater lakes and the brackish Baltic Sea, it is females that tend to dominate. As a rule, yellow eels tend to be more common in shallow brackish water along protected coasts, and in fjords and bays, than in freshwater or the open sea.

Eels at most of their life stages seem to be negatively phototrophic, preferring darker habitats. They have a remarkably acute sense of smell, their specialised olfactory organ being five times the size of other freshwater fish and used to find prey, mainly at night. Another notable characteristic is their ability to survive more than 24 h out of water, allowing them to travel over land through wet vegetation when necessary, for example when migrating from isolated pockets of freshwater into rivers during the early stages of their spawning migration.

After some 6–20 years in fresh or brackish water, but depending on sex and physical state, the silvering process starts, indicating the onset of sexual maturation. During this process the eels adopt the silver form, with enlarged eyes and a light metallic abdominal colour, and they cease feeding. The main spawning migration takes place from late summer to early winter in Denmark, but migrating eels may be encountered too in spring. Moon phases seem to play an important role in the migration, but factors such as intensity of water flow are apparently equally important. During the silvering process, gonad maturation is inhibited, and maturation seems to be resumed only when approaching the Sargasso Sea. Eels are assumed to die after spawning because adult eels have never been observed in the Sargasso Sea or returning across the Atlantic.

Eel Habitat and Distribution in Denmark

Denmark is a small, flat country, with an area of ~43,000 km^2, and its highest point is just 173 m above sea level. Its coastline including all islands and fjords exceeds 7,300 km, and no place is more than 50 km from the nearest coast (Fig. 3.2). As there are no natural barriers to eel migration in Denmark, eels are found in virtually all freshwater rivers, streams, ponds and lakes as well as in brackish water along the coastline and in fjords. However, the Danish mainland and its islands are intensively cultivated or in other ways influenced by human activity, which has reduced natural eel habitats in both number and quality.

Wetlands have been drained and watercourses straightened and regulated, often with constructions hampering eel migration. Lakes, fjords and shallow coastal areas are subject to nutrient run-off from cultivated soils via freshwater streams, which through eutrophication may cause oxygen depletion in warm summers. Eels are sensitive to such oxygen depletion, although they may survive anoxic conditions for a short time. Efforts are now ongoing in Denmark as elsewhere to restore habitats and to reduce nutrient run-off to the aquatic environment, in support of recent management plans required by the European Union (EU) to aid recovery of the European eel.

The Status of Eels and Their Management

The European eel has declined significantly and is at a historical low throughout its distribution. Its decline is believed to have been caused by a combination of fishing pressure at all continental life stages (glass, yellow and silver eels), deterioration of habitats, including drainage of wetlands, the installation of hydro-electric plants and other barriers to up- and downstream river migration, pollution and introduced diseases and parasites. Eels were abundant in Danish waters until some 50 years ago, as much as 3,000–5,000 t of yellow and silver eels being taken annually between 1920 and 1970; by 2010, however, the annual catch was <400 t (Fig. 3.3). Seasonal runs of glass eels to Denmark are now very small and the recruitment of yellow eels to Danish streams is <5 % of that in the 1970s (ICES 2009a). Based on the state of the stock Europe-wide, the International Council for the Exploration of the Sea (ICES) recommends that "all anthropogenic impacts on production and escapement of eels should be reduced to as close to zero as possible until stock recovery is achieved" (ICES 2009b), and the European eel is now included in both the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Freyhof and Kottelat 2010) and the Danish Red List as "Critically Endangered" (Wind and Pihl 2004).

Fig. 3.2 A map of Denmark, showing its many fjords, bays and islands, which together create a coastline >7,300 km long

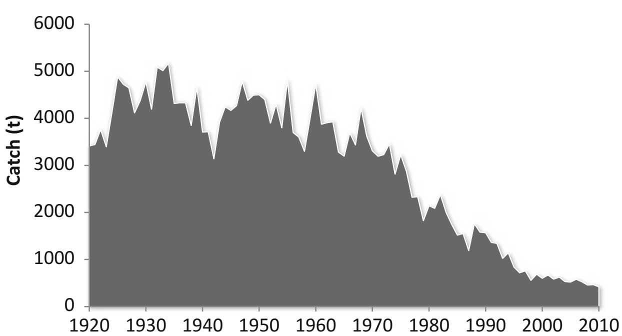

Fig. 3.3 Danish eel catches, 1920–2010 (statistics courtesy Danish AgriFish Agency, Danish Ministry of Food, Agriculture and Fisheries)

In 2007 a framework regulation for the recovery of the European eel was endorsed by the EU (European Union 2007), aimed at protecting and improving the possibility of future sustainable exploitation of the species. In terms of that framework agreement, each EU Member State is required to establish eel management plans for recovering the European eel population. The EU Council Regulation was implemented in Denmark in 2009 (Anon 2008). The Danish eel management plan consists of two primary elements: a plan for inland freshwater aiming at a 40 % escapement level (relative to pristine) for silver eels to the sea, and a management plan for marine waters reducing the fishing effort by at least 50 % relative to the average annual effort between 2004 and 2006. The measures proposed to attain these goals include a licensing system for professional fisheries and a shorter fishing season for recreational fishers. In freshwater, the measures further include restocking based on farmed glass eels, and in marine waters, an increase in the minimum legal capture size for yellow eels to 40 cm. Other measures in the plan include restrictions on fishing gear and season, catch registration, consideration of obstructions to migration, improvement of eel habitats, and restocking. Current adjustments to the measures are part of the plan, and depending on stock development trends, all inland eel fisheries may be phased out by the end of 2013.

Eel Fisheries in Denmark

The eel has been fished as long as there have been people in Denmark, and for good reason. The species was, at least until 50 years ago, abundant and distributed widely; it is fat and tasty, can be kept alive easily, is caught with simple fishing gear, is available year-round, and has a predictable migration pattern. There is archaeological evidence in Denmark that eels were being captured by pot (Fig. 3.4) and spear and used as a source of food in the Stone Age (~5000–4000 BC).

Up to World War 2, fishing for eels in Denmark was typically performed by smallholder farmers, who fished for eels to supply the household with food or extra income. After World War 2, however, the practice changed and professional fishing for eels gained popularity with the use of trawls, nylon nets and larger poundnets; catches were sometimes huge. However, as the stock and the catches dwindled, so did the number of commercial fishers, and nowadays only a few are involved in professional eel fisheries (Sparrevohn et al. 2011). Many more recreational fishers catch eels in Denmark, though, perhaps as many as 15,000, but the types of gear that they can use are restricted and purchase of their catches is illegal. Recent surveys estimated that recreational fishers may catch some 100 t of eels annually (Sparrevohn et al. 2011), an amount not accounted for in the annual 400 t commercial catch.

Most Danish eel fisheries, commercial and recreational, operate in the brackish coastal waters of shallow fjords and bays, where eel density is greatest, and just 5 % of the catches reported are derived from freshwater. The Danish fishery targets yellow and silver eels, with fisheries on yellow eels between spring and early autumn and on silver eels between late summer and late autumn. The main fishing seasons for yellow and silver eels depend, however, on factors such as temperature, weather, water flow and discharge. Most commercial eel fisheries are concentrated in southern and eastern Denmark, where silver eels pass through the narrow Straits of Denmark as they migrate from the Baltic Sea towards the North Sea and Atlantic, and ultimately the spawning area in the Sargasso Sea.

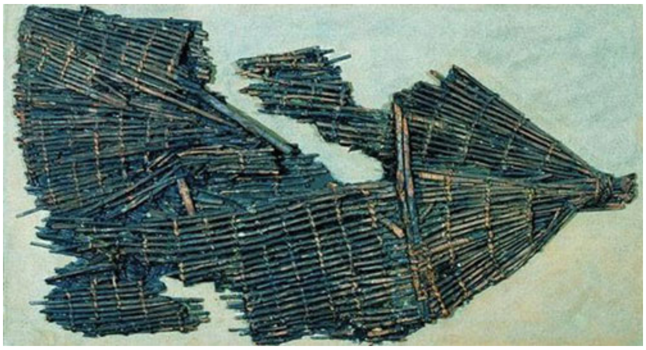

Fig. 3.4 A fish pot made of woven osiers from the early Stone Age. The pot, once used for eel fishing, was found in a bog near the town of Holbaek in Zealand, Denmark, and is today exhibited at the National Museum of Denmark. This type of fishing gear has been used almost unaltered until today, either alone or as part of an eel trap (from www.denstoredanske.dk; Danish open encyclopaedia)

Traditional Fishing Gear and Methods

A wealth of methods and equipment has been developed and used for fishing eels. In Denmark, the gears used through time include a variety of spear types, eel pots and traps, rod and line, longlines, pound-, fyke- and seinenets, and trawls. The use of some gear types, e.g. spears (Fig. 3.5), stopped long ago, and other types were prohibited more recently as part of the regulation of fisheries. Since 2009, for instance, the use of driftnets, trawls and seines has been prohibited and seasonal closures have been implemented for all remaining fisheries. Recreational fishing has been strictly limited in terms of gear and operating season.

An *eel pot* is an ancient fishing gear that has persisted almost unaltered over time, but it is rarely used today. The oldest known eel baskets found in Denmark were woven from osier (Fig. 3.4); today they are made of synthetic fibre or plastic. An eel pot can be used alone or in connection with a *fykenet* (Fig. 3.5 bottom left), individually deployed in streams or lakes. *Eel spears* (Fig. 3.5 top left) were used mainly from boats during summer, but winter eelers in the past would also catch eels through holes in the ice (Fig. 3.1). Spears were then thrust into the muddy bottom to catch the eels. Different types of spear were used depending on the nature of the bottom and the size of the eels being targeted. In Denmark, all types of spear are now prohibited, because they harm the eels and prevent the successful release of undersized fish.

A traditional way of catching eels in shallow water in the fjords and freshwater especially in northern Denmark was eel *pushnets* or *push traps* (Fig. 3.5 top right). To operate them, two people worked together, one working the bottom and disturbing the resting eels, chasing them into the pushnet, the other lifting the net as soon as an eel entered it. The catch was kept in a basket carried around on the shoulders of the operators. *Eel weirs* (Fig. 3.5 bottom right) are no longer used in Denmark, although they were until a few decades ago. A bridge on top of the leader made it convenient to harvest eels from the eel pot at its end. The legal right to fish with them belonged to the owner of the coastal land, but nowadays there are no private fishing rights at the coast. In some places there are wooden *eel traps* (Fig. 3.6), built at the outflow of lakes or on weirs in rivers to catch the silver eels migrating downstream during autumn. All such traps are registered and their use restricted by seasonal closure. From the end of 2013, however, their use will be prohibited completely.

Longlines may operate with 100 or more hooks baited with fresh worms, shrimps or small fish. Lines are set in the evening and checked before sunrise. The use of such longlines is still legal in some areas, but not in others. In earlier times, a simpler but not necessarily easy way to catch eels on a line was *bobbing* (peuren in the Netherlands), which required 10–20 earthworms to be coiled into a ball on a thin thread fastened to a string at the end of a rod. When the bait was lowered into the water, an eel would bite it and before it let go, would be lifted into the boat; great skill was required to fish in this way!

Poundnets are probably the most commonly used type of gear in recent time, especially in the straits connecting the Baltic with the North Sea, where they effectively catch migrating silver eels. When the fishery was most intense, poundnets were placed strategically just 500 m apart over many kilometres. For poundnets targeting silver eels (Fig. 3.7 top), which are legal only for professional fishers, the diameter of the enclosure is typically >20 m and the headline up to 500 m long. The latter is fixed on piles or attached to buoys. The nets themselves are constructed to fit individual fishing sites and can be quite large, sometimes extending from the surface to depths of 16 m. *Fykenets* (Fig. 3.5 bottom left and Fig. 3.7 bottom) are smaller and have no enclosure, and the headline is typically <50 m long. Their headline too is fixed on piles or attached to buoys. Both pound- and fykenets are still operated all around Denmark, and in fjords and lakes, most often in mixed fisheries, but there are tight restrictions on their use. The use of *driftnets* (Fig. 3.8), *seines* (which can also be deployed from shore) and *trawls* to catch eels is now prohibited in Denmark.

Fishing Boats

Eel drifters were developed and built from 1880 to 1930 exclusively to fish for eels (Fig. 3.8). They were classic Danish, clinker-built boats, constructed so that they could drift sideways with an extended seinenet drifting out from their side. When the centreboard was lifted, the flat-bottomed vessel

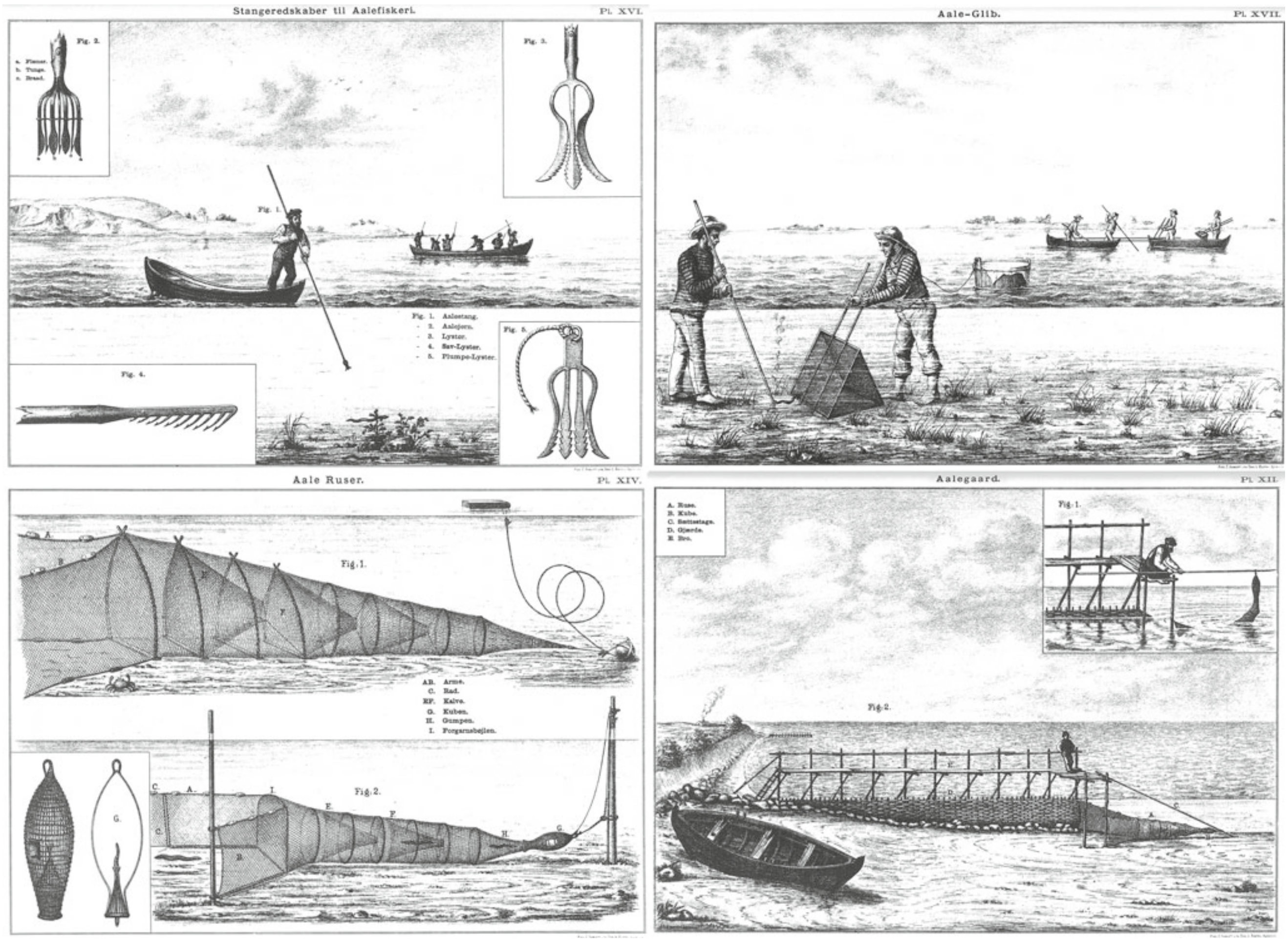

Fig. 3.5 Early types of gear used to fish eels: eel spears (*top left*), eel pushnet (*top right*), a selection of fykenets (*bottom left*) and an eel weir (*bottom right*) (from Drechsel 1890)

Fig. 3.6 A freshwater eel trap at the stream leading from Lake Vandet in Thy National Park, Denmark, used to catch migrating silver eels (photograph, Sune Riis Sørensen, DTU Aqua)

would simply drift sideways, dragging the net along the seabed. The catch was kept alive in a well amidships. However, with the introduction of motorized boats, such drifters were consigned to history as far as fishing was concerned. Some 10 eel drifters still exist, though, and they are used for recreation because of their fine sailing abilities (Fig. 3.9).

Restocking of Eels

During industrial and agricultural development in the eighteenth and nineteenth centuries, many river systems were altered by dam construction for hydro-electric power production or weir building to control water levels, and both created barriers to eel migration. To mitigate the effect of such barriers, however, it has been statutory in Denmark since 1898 to install eel passes at the barriers. In the past, elvers and yellow eels were stocked by fishers in inland waters, in places where recruitment was low; indeed, from the mid-1960s to the end of the 1980s, licences were granted to catch and sell eels for stocking purposes. Such stocking and transfer of eels was then prohibited as a consequence of the poor recruitment in the wild and to prevent the spread of

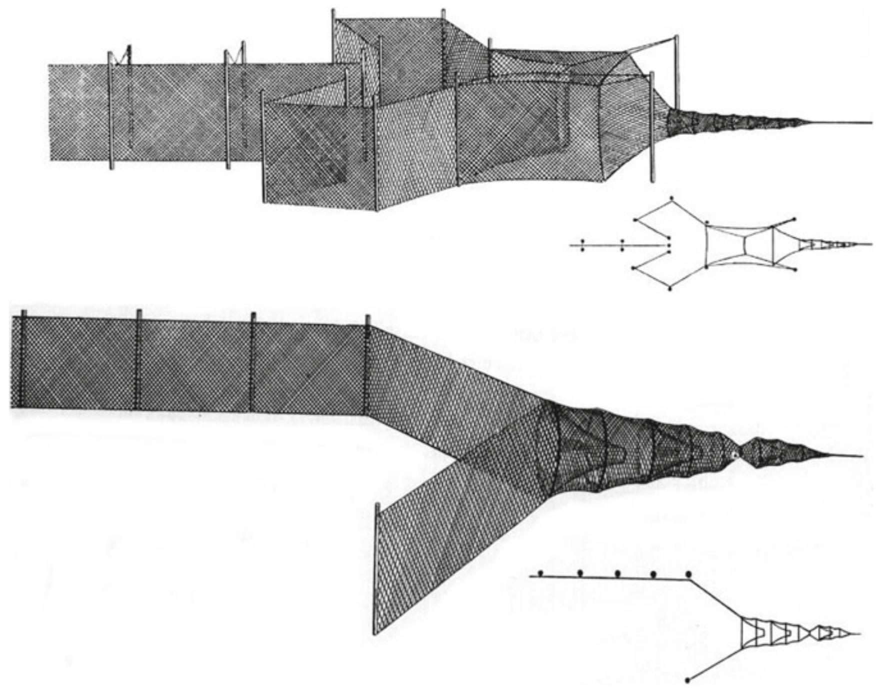

Fig. 3.7 A typical present day poundnet (*top*) and fykenet (*bottom*) used for catching eels (from Anon 2008)

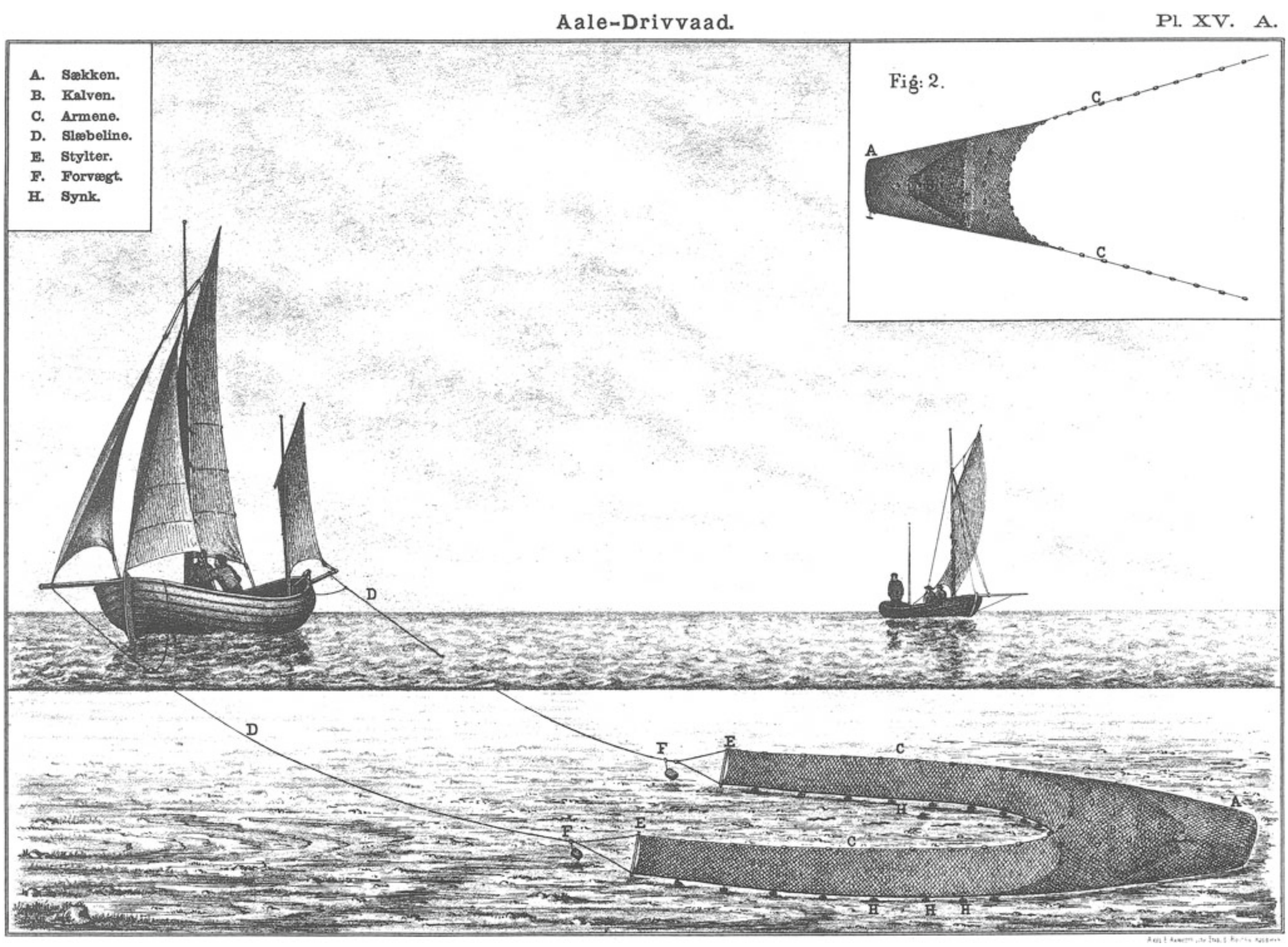

Fig. 3.8 An eel drifter with a driftnet (from Drechsel 1890)

Fig. 3.9 Eel drifters now used for recreational sailing: "Concordia", in private ownership (*left* and *centre*) and "Viktoria" owned by the Viking Ship Museum (*right*). (Photographs left and centre, Suzanne Rindom, DTU Aqua; right, Werner Karrasch, © The Viking Ship Museum, Roskilde, Denmark)

the eel swimbladder worm *Anguillicoloides crassus*, which was introduced accidentally to Europe from Asia during the 1980s. Since 1987, however, the Danish Government and the recreational fishing licence fee have financially supported a controlled restocking programme (Kirkegaard 2010), using wild-caught glass eels imported mainly from France and grown to a weight of 2–5 g (fingerlings) before release. Recently, the quantity stocked has declined, following the escalation in the price of glass eels. In 2010, 1.54 million fingerlings were stocked in Danish lakes, rivers and coastal areas.

Eels in Aquaculture in Denmark

Eels have been farmed in Denmark for centuries. Initially, there was no distinction between restocking and farming, and eels were moved around as glass eels, fingerlings and elvers, often using ponds for farming purposes. The eels were fed many types of feed, but mainly fish waste. A problem with farming in ponds, however, is the eel's ability to escape over land through wet grass, hence at times leaving farmers with no eels to harvest!

In the late 1970s, first attempts were made to farm eels in indoor aquaculture facilities using recirculation technology (Kirkegaard 2010). Such facilities were often established in existing buildings and consisted of fish tanks, a reservoir, a pump and submerged filters (which allowed bacteria to remove waste products from fish by nitrification of the ammonia), supplemented with an oxygenating device. Many such systems were built during the 1980s, but they required a huge amount of water, as much as 1,000 l kg^{-1} of feed. Also, the water had to be heated to ~25 °C, which even in those days was financially challenging. Later, therefore, microsieves were introduced to remove particles prior to cleansing by the submerged filters, and ultraviolet light was employed to sterilize the water. A modern-day purpose-built eel aquaculture facility and a filtration plant are shown in Fig. 3.10. The main reason for the huge quantity of water needed in the process was the nitrate created by nitrification at the submerged filters, so farms started to use denitrification technology too. Nowadays, with this technology, <100 l of water are needed per kg of feed, and some farms have also introduced phosphorus systems, reducing the water requirement to <50 l kg^{-1} of feed.

Glass Eels and Farming

Aquaculture eel production is currently based exclusively on wild-caught glass eels, which for the European eel are fished in estuaries and rivers mainly in the Bay of Biscay and the UK's River Severn (Kirkegaard 2010). Like everywhere else, though, catches of glass eels there have decreased dramatically over the past 50 years, in France for instance dropping from >500 t in 1995 to ~50 t in 2011. During those 15 years too, Chinese eel culturists have shown great interest in purchasing European glass eels, because Japanese glass eels (*Anguilla japonica*) tend to be up to ten times more expensive than European ones.

Fig. 3.10 Fish tanks at a Danish eel farm (*top*), and a filter unit with submerged and trickling filters, oxygen cones, pumps, UV-sterilizer, micro-sieve and pumps (photographs, Christian Graver, Danish Eel Farmers Association)

Increased competition has therefore driven up the price of European glass eels from €200 to as much as €1,100 per kg, although prices are generally fairly stable at ~€400–600 per kg. Trading restrictions are now implemented to protect the European eel.

The continuing decline in the catch of glass eels naturally stimulated the various research initiatives underway in Europe and elsewhere in the world to develop a self-sustained culture of eels, focusing on breeding programmes for aquaculture. This subject is addressed also elsewhere in this book.

Eel Production, Markets and Restocking

During the 1980s, most Danish aquaculture production came from small, family-owned businesses delivering between 1 and 10 t annually. Then, during the 1990s and into the twenty-first century, the number of eel farms decreased, and the average annual production of each of the remaining businesses grew. In 1990, for instance, there were 47 eel farms in Denmark with an average annual production of 12.5 t; by 2011 the number had dwindled to just eight, however, with an average annual production of ~250 t.

Most of the eels produced in Denmark for human consumption are exported to the Netherlands. Dutch smokehouses prefer eels of ~145 g for smoking and filleting; eels >400 g are smoked in Denmark or exported to Germany. A substantial proportion of glass eels entering current aquaculture in Denmark is used in the production of fingerlings to restock Danish and other northern European water bodies; this includes several million fingerlings of 2–10 g that are exported to Germany and Poland.

Danish Eel Research

Denmark has a long tradition of research into the biology and ecology of the European eel. Past and present research areas include the identification of spawning areas, silver eel migration and analyses of the factors that influence larval drift and development, along with population genetics and studies on the reproduction of eels in captivity.

Johannes Schmidt's Research

Johannes Schmidt (see box) is renowned for his research during the period 1904–1922 outlining the spawning area of the European eel. His great interest in finding the spawning areas and larval drift routes was aroused when he caught a leptocephalus larva off the Faroe Islands in 1904. Eight years before, in 1896, the Italian zoologist Giovanni Grassi had been the first to identify eel larvae by observing the transformation of a leptocephalus (formerly believed to be a unique species) into a glass eel (Grassi 1896), and suggested that spawning took place in deep waters of the Mediterranean Sea. However, on finding eel larvae in the Atlantic, Schmidt argued that at least some spawning areas would be in the Atlantic itself. Dedicated to resolving the enigma of eel reproduction, he initiated a Danish research programme that focused on identifying the spawning areas of European eel, and because of the importance of the eel to Denmark, he attracted financial support for a campaign that eventually lasted for two decades, interrupted only by World War 1.

In the early 1900s, researchers had succeeded in documenting the spawning areas, stock distributions and spawning migrations of various fish species. During his early work on other species, notably Atlantic cod (*Gadus morhua*), Schmidt had worked with methods for identifying fish spawning areas, including the development of gear that effectively sampled fish eggs and larvae, so he systematically sampled eel larvae over large areas of the Atlantic, obtaining information on species composition and larval length. Then, by back-tracking larval size to the locations where the smallest larvae were caught, he mapped drift patterns and delimited the spawning area of the European eel as the Sargasso Sea.

Schmidt attempted to publish his initial results in 1912, but he was not acknowledged for his findings at that time, because confirmation of the delimitation of the exact area of spawning was required. In fact, he was refused the opportunity to publish his results in the Proceedings of the Royal Society, the obvious scientific medium then for publishing results of such importance. He carried out a cruise in 1913 to the western Atlantic, but World War 1 came and 7 years passed before he had another opportunity to return to the Sargasso Sea. That survey took place in 1920/1921 on a schooner placed at his disposal by a privately owned trading company, the East Asiatic Company of Copenhagen. During the survey he sampled larvae in the area he had earlier identified to be the spawning area of both American (*Anguilla rostrata*) and European eels, and he then delimited the area by collating the information obtained during this and preceding surveys. Finally, in 1922, he published the work on eel larval abundance and size across the entire North Atlantic (Fig. 3.11) for which he later became famous (Schmidt 1922); in this he defined the spawning area of both European and American eels as the southern Sargasso Sea, based on a relatively narrow band of very small larvae centred around latitude 26°N. Another important result from his studies was a description of the increase in size and development of the growing leptocephalus larvae over time as they drifted from the spawning site towards the European continent.

Danish Field Research, 1966–2007

Danish interest in eel research was maintained after Schmidt's death in 1933, and his material, supplemented with new material from the eastern Atlantic, was analysed further. However, it was not until 1966 that another Danish field expedition set out for the Sargasso Sea with focus on the eastern part of the hitherto identified spawning area of the European eel, where small eel larvae had been found as far east as ~57°W.

During the 1970s and 1980s, several countries carried out research cruises to the Sargasso Sea, collecting new information on the distribution of eel larvae, and it became clear that

Professor Doctor Phil. Johannes Schmidt

Ernst Johannes Schmidt is one of Denmark's best known marine scientists and his work is respected worldwide, in particular his research on eels. He was born on 2 January 1877 (Bruun 1934), received a master's degree in natural history in 1898 and a doctoral degree in botany in 1903. Also in 1903, he married Ingeborg Kühle, daughter of the director of the Carlsberg Co. (Reagan 1933). During 1901 and 1902 he worked as an assistant at the Danish Biological Station, where his interest in marine science was stimulated by Prof. C. G. J. Petersen, then from 1902 to 1909 part-time for the Botanical Institute of the University of Copenhagen and part-time for the Danish Commission for Investigation of the Sea, on marine science. In 1910, he was made head of the department of physiology at the Carlsberg Laboratory, a post he held until his death on 21 February 1933 (Bruun 1934).

Johannes Schmidt (photo © Polfoto, Copenhagen, Denmark)

In his early research, Schmidt clarified aspects of the early life of commercial fish, especially cod. In 1903, however, he expanded his geographic horizons to cover the southern areas of the North Atlantic, where he collected large numbers of pelagic fish larvae around the Faroe Islands and Iceland. This material provided new, detailed knowledge about North Atlantic fish species during all their life stages, from eggs and larvae to adults, as well as information on spawning areas and seasons. It is, however, for his work on eels that Johannes Schmidt will be remembered best (Bruun 1934). After catching a single eel larva in the Atlantic in May 1904, he devoted the rest of his working life to solving the mystery of eel reproduction. His work ultimately led to the discovery that Atlantic eels breed in the Sargasso Sea, finally presenting proof of this in 1922 (Reagan 1933). Then, having demonstrated where Atlantic eels spawn, Schmidt turned his attention to other parts of the world. He travelled to Australia, New Zealand and Tahiti to study the eels of the Pacific, and it was those studies that fuelled his desire to map the spawning and larval stages of eels other than the Atlantic species. A large grant from the Carlsberg Foundation along with considerable state subsidies then supported him on a circumnavigation of the world in the steamer "Dana." The ship left Copenhagen on 14 June 1928 for the Mediterranean, crossed the Atlantic, passed through the Panama Canal, went past the Pacific Islands en route to New Zealand and Australia, and from there steamed on to China, New Guinea and Sumatra, across the Indian Ocean to Madagascar and East Africa, around the Cape of Good Hope, then back north through the Atlantic, arriving back in Copenhagen on 30 June 1930. Schmidt brought back large collections of marine fauna (Winge and Tåning 1947), which now reside in the Zoological Museum in Copenhagen, many open for public view. The Danish newspaper "Politiken" wrote under the headline *The "Dana" returns home after two-year voyage*[1]:

> Yesterday afternoon at about 2 pm, a small, grey steamer glided into Copenhagen harbour and set a course down past Langelinie. At the time there was a large welcoming committee awaiting it, at the Custom House. Reading the name "Dana" on the bows, those watching realized that it was the expedition that had set out 2 years before to investigate the riddles of the seven seas and which, under Professor Schmidt's leadership, had made Denmark's name known right round the world and boosted her reputation in the field of international ocean research.
>
> We managed to pull Professor Schmidt aside and asked him to tell us a little about the results of the voyage: "what do you consider to be the expedition's most important result?" "It will take a long time before that question can be answered", replied Prof. Schmidt. "Not until all the material has been analysed carefully will we be able to say for certain, but as far as I can tell at the moment, I believe that our research into the life and activities of the eel will be the most significant outcome".

[1] Selected passages from the Danish newspaper article "The Dana returns home after two-year voyage", issued in "Politiken" 1 July 1930, translated into English by Pete Westbrook, then paraphrased.

The "Dana" returns home after a 2-year voyage. Ocean research expedition brings back a huge amount of material that will take 5 years to collate (photo courtesy DTU Aqua, Denmark)

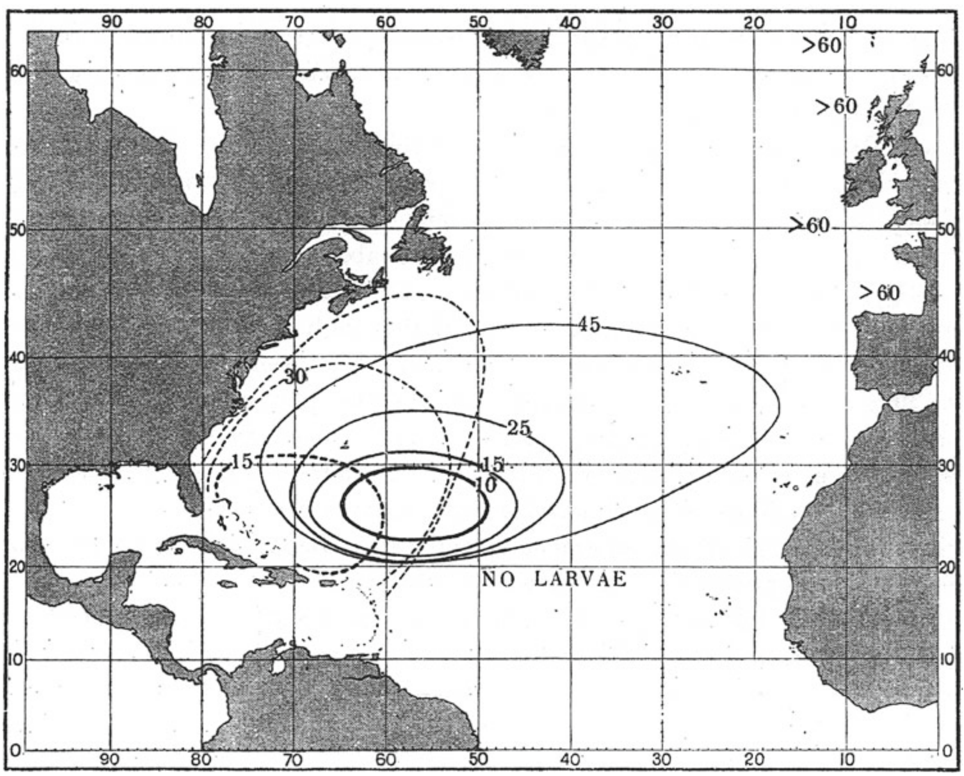

Fig. 3.11 European and American eel spawning areas, with the distributions of larvae of different size indicated by *curves* (*dotted* for American, *continuous lines* for European). The *heavily-drawn innermost curves* embrace the spawning areas of the two species, and the curves drawn progressively outwards from the spawning areas show the limits of occurrence of 25 mm specimens, etc. (from Schmidt 1922)

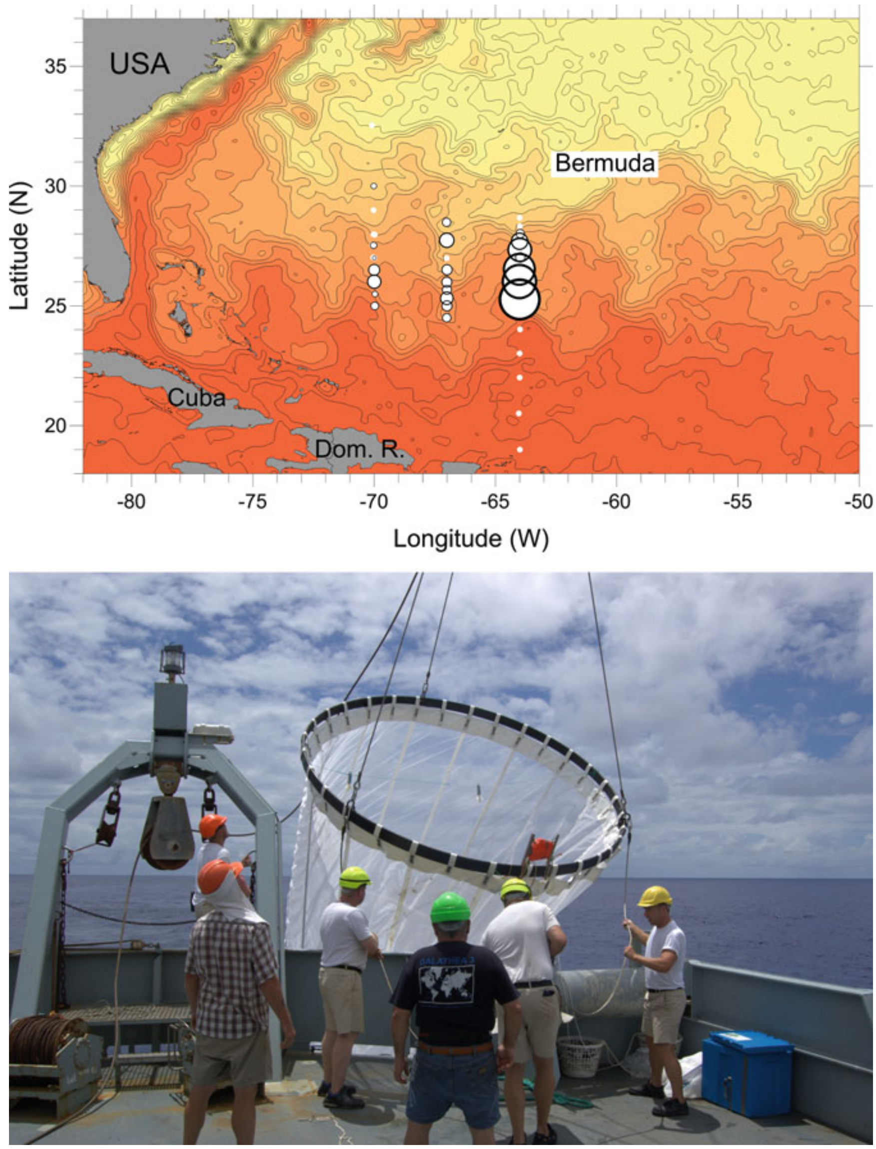

Fig. 3.12 *Top*: Satellite image of the Atlantic Ocean in April 2007, illustrating where warmer subtropical water (*red*) meets cooler northern water (*yellow*), indicating the frontal zones. The *white dots* illustrate the sampling for larvae in 2007, and *black circles* depict the abundance of European eel larvae (graphics courtesy Peter Munk, DTU Aqua). *Bottom:* The plankton net is hoisted on board the RV "Vædderen" during a haul in the Atlantic Ocean in 2007 (photograph, Peter Munk, DTU Aqua)

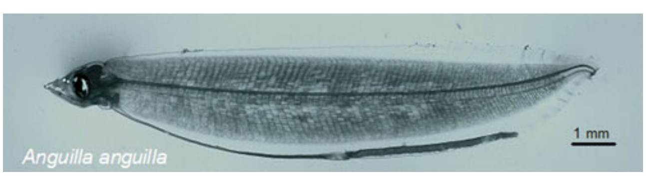

Fig. 3.13 A European eel larva (photograph, Peter Munk, DTU Aqua)

the distribution of small larvae, and consequently eel spawning, was related to the unique hydrography of that part of the Atlantic. There, warm tropical surface water meets cooler water from the North Atlantic and forms a front at the subtropical convergence, and it is there that the abundance of small eel larvae appears to be greatest (Fig. 3.12 top).

In 2007, a new investigation was carried out as part of the Danish Galathea 3 World Expedition. The research led to enhanced understanding of the location of eel spawning areas, larval life history and the potential influences of climate-induced environmental changes. During a cruise in March–April 2007, the RV "Vædderen" worked in the Sargasso Sea (Fig. 3.12 top). Transects crossed the fronts of the subtropical convergence with the aim of investigating hydrography, chemistry and plankton biology and intensively sampling for eel larvae (Fig. 3.12 bottom). Both American and European eel larvae were caught in the frontal zone, with sizes as small as 5 mm, though the average size was ~12 mm (Fig. 3.13). The findings underscored the importance of oceanic frontal processes in retaining eel larvae within areas of good food availability and in directing their drift towards continental land masses (Munk et al. 2010). As Schmidt had shown earlier, American eel larvae dominated in the western part of the area investigated and

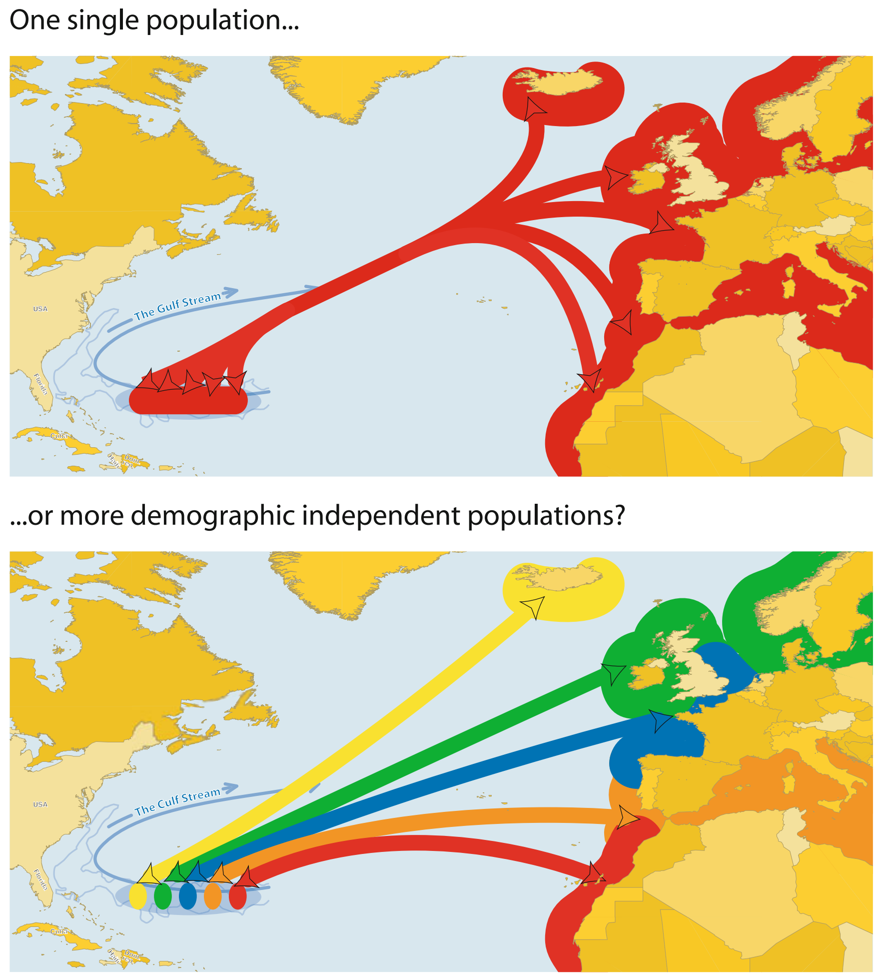

Fig. 3.14 An illustration of the two distribution theories for the European eel, panmixia (*top*) and genetic differentiation between populations (*bottom*). Graphics courtesy Thomas Dam Als, DTU Aqua

European eel larvae towards the east. Hence, it is likely that most of the American eel larvae will drift west or north in the Antilles Current, and that European eel larvae will tend to follow an eastward route toward the Azores and Europe, because of their more easterly distribution close to the east-flowing current associated with the front (Munk et al. 2010). Clearly, therefore, the life history, survival and drift of European and American eel larvae will depend strongly on climate-related oceanographic processes.

The European Eel: One or More Populations?

Another question central to the management and conservation of Atlantic eels is whether there is a single population or several smaller, demographically independent ones.

European and American eels appear to spawn in partially overlapping areas in the Sargasso Sea, with larvae of the American eel drifting ~2,000 km to North America and their European equivalents drifting >5,000 km to the coasts of Europe and North Africa. Several aspects of eel biology, including their long-distance spawning migration and subsequent lengthy larval transport by ocean currents, suggest that all individuals of each species target the same spawning area and mate independent of origin, despite such random mating being rare in geographically widespread species. Hence, both European and American eels represent classic textbook examples of panmictic species, each comprising a single, randomly mating population.

Schmidt separated European and American eels on the basis of the number of vertebrae, and he observed no geographic differentiation within either species, supporting the panmixia hypothesis (Schmidt 1922). More recently, the results of genetic studies of populations of the European eel (Fig. 3.14) have fuelled controversy. Early genetic studies supported panmixia in both species, but some later studies using novel genetic markers yielded evidence against panmixia, by suggesting isolation of populations by either migration distance or time. One set of studies found significant genetic differentiation between geographically distinct samples of glass eels, but another that indicated isolation by time found temporal genetic differentiation between different arrival waves of glass eels, presumably caused by differences in spawning time among spawning groups in the Sargasso Sea (Wirth and Bernatchez 2001; Dannewitz et al. 2005). Common for most of these studies is that they were based exclusively on continental samples and not on samples from the spawning area. Als et al. (2011), however, provide a comprehensive genetic dataset on European eels based on samples of larvae collected from the Sargasso Sea during the Danish Galathea 3 Expedition in 2007, along with glass eels sampled from continental areas between Iceland and Morocco. In that study, no evidence was found for isolation by either distance or time, and all results accord with the panmixia hypothesis, so on the basis of those results, it is likely that all silver eels of a species share a common spawning area and that European eel larvae subsequently distribute randomly across the whole European and North African distribution area.

Several aspects of the life history of the European eel fit this scenario (Als et al. 2011). (i) Long-distance transport of eel larvae by ocean currents to foraging areas used by elvers and yellow eels provides plenty of opportunity for mixing of larvae from different parts of the spawning area. (ii) Precise homing of silver eels to specific natal sites in the Sargasso Sea appears unlikely, because that would conflict with the necessity to spawn in dynamic, undulating thermal fronts. (iii) Imprinting and homing to lower-water-column parts of the 5,000-m-deep Sargasso Sea is unlikely, because migration, spawning and larval drift takes place in the upper pelagic zone of the ocean (<1,000 m deep).

Hence, the study concludes that European eels likely do not exhibit fine-scale homing towards their precise natal sites, but rather a crude homing behaviour towards the frontal zones of the Sargasso Sea (Als et al. 2011). The finding that all European eels form a single population points to the need for management and conservation effort to be coordinated at a transnational level; overexploitation in one region would negatively influence the whole population of European eels and depress recruitment across the entire distributional range of the species.

European Eel Migration: Following Silver Eels to Their Spawning Area

One of the main mysteries about eels is what happens when the silver eels leave the coasts of Europe never to return. Some eels have been caught incidentally in trawls south of the Faroe Islands and off the Azores, and a few have been identified in the stomach contents of humpback whales. Knowledge of the migration behaviour or route of the eels is still incomplete, however, and no-one has yet caught a spawning eel in the Sargasso Sea.

Fig. 3.15 A female silver eel with a pop-up satellite archival tag (PSAT), released at the west coast of Ireland after tagging (image from a video recorded by Robert Schabetsberger and Ingo Eichelberger, Austria)

Because of the very long distances European eels migrate (up to 7,000 km) over possible water depths of >5,000 m, a traditional fishery approach to studying migration is not feasible. An alternative way to track migration is by telemetry, i.e. by attaching a tag to the animal. Radio tags do not work in saline water, but acoustic tags do and have been applied to eels, though the results are limited by the restricted range of signal transmission. Recently, however, modern Pop-up Satellite Archival Tags (PSATs) have proven successful in documenting eel migration (though see the discussion on the subject elsewhere in this book). PSATs are used widely to track the movements of bigger animals that live in the upper few hundred metres of the ocean and that typically travel great distances, which makes them difficult to study in any other way. Tags are mounted on the animal and store data such as temperature, depth and light level. At a predetermined time, the tags initiate a release mechanism and "pop off" the animal, float to the surface and relay their data to ARGOS satellites, and that information can then be downloaded via the ARGOS system.

During the Danish Galathea 3 Expedition in 2007, researchers attempted to determine the transoceanic migration routes and behaviour of migrating silver eels and to test the concept of PSAT tagging in a large-scale field programme (Aarestrup et al. 2009). In order to obtain large eels for tagging, almost 100,000 eels were captured. Of these, 22 large wild female silver eels were selected and tagged with a small PSAT mounted on their backs, with a specially developed attachment securing the PSAT to the eels, like backpacks (Fig. 3.15). All were released on the west coast of Ireland in

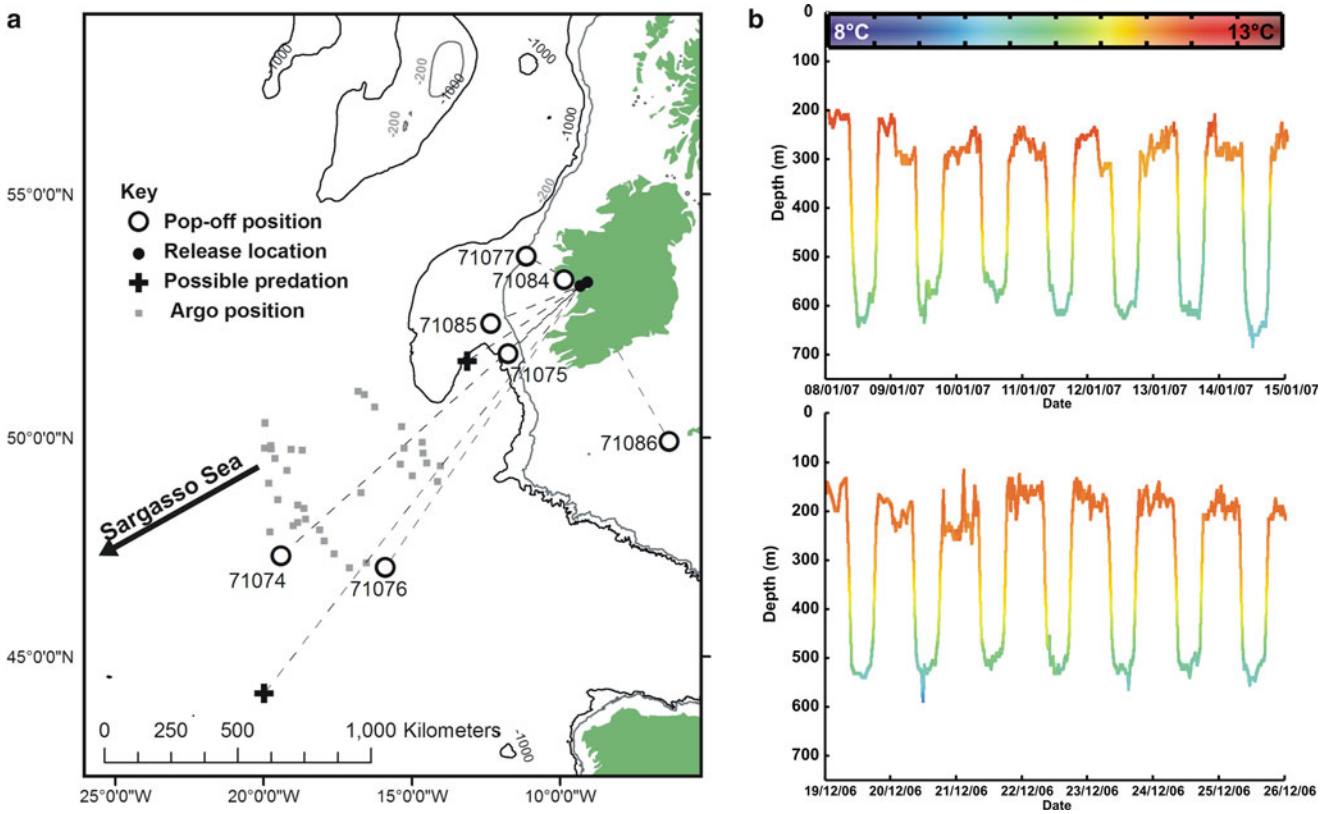

Fig. 3.16 (**a**) Map showing the pop-up positions for the PSATs. (**b**) and (**c**) Vertical migration of two eels over a week, with depth values coloured by temperature (from Aarestrup et al. 2009, reproduced with permission)

October and November 2007 during their normal migration season there. The PSATs were programmed to be released from the eel at a pre-set time, and although the full migration route was not completed, some tantalising insights were gained. The eels on leaving Ireland seemed to take a southwesterly route towards the Azores (Fig. 3.16a), south of the line they would have taken had they been heading directly for the Sargasso Sea, possibly to take advantage of favourable current systems and hence to save stored energy for reproduction. The study also demonstrated (Fig. 3.16b, c) that the silver eels migrated closer to the surface at night and deeper by day, once the eels had left the continental shelf and were in oceanic water often thousands of metres deep. Such a pattern, known as diel vertical migration, is not uncommon in marine organisms and is thought to be an adaptation evolved mainly as a trade-off between feeding and predation avoidance. By day, animals dive deep to avoid predators, but at night when predation risks should be lower, they rise towards the surface to feed in the more productive layers of the water column. The deep dives by day seem to make sense for eels, which obviously wish to lessen their risk of predation, but silver eels do not feed at all while migrating, so why they swim closer to the surface at night is not clear. Such behaviour may have something to do with controlling the maturation process, or it could be that eels use some type of migration cue that is only found closer to the surface. More research is needed to yield answers to these questions.

The general hypothesis for eel migration is that silver eels leave Europe in autumn to spawn in the Sargasso Sea the following spring. Based on this belief and the distance they have to travel, the minimum migration speed can be calculated, but the speed of the PSAT-tagged eels in that study was less than the speed needed to complete the migration in that time. The reason for this can be either that the PSATs slow down the eels (as suggested elsewhere in this book), or that the eels take longer than hypothesized to complete their journey to the Sargasso Sea. European scientists, e.g. in the EU project EELIAD, have undertaken large-scale studies into eel migration, including alternative tagging methods. Experiments have been conducted with implanted tags, to preclude concerns that the eels may be slowed down by the drag caused by external attachment of tags. The principle in this work is that when the eel dies, after spawning or as a result of predation during migration, the tag would rise to the surface, drift shorewards and hopefully be recovered and returned to the address stated on the tag. Then, stored data such as temperature and depth will provide detailed

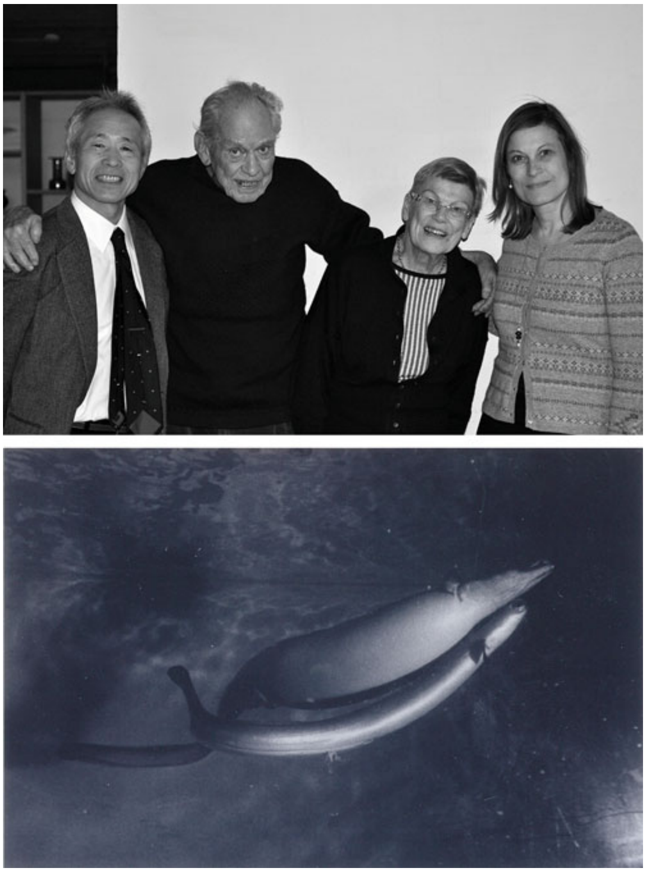

Fig. 3.17 *Top:* Inge Boëtius (86 in 2011) and Jan Boëtius (94) still have interest in the biology of eels and are happy to share their knowledge with other researchers. From left, guest editor Katsumi Tsukamoto, University of Tokyo, Jan Boëtius, Inge Boëtius, Jonna Tomkiewicz, DTU Aqua (photograph, guest editor Mari Kuroki, The University of Tokyo). *Bottom:* The well-known photograph "Eels in love", of a spawning-ready female European eel being courted by a smaller male eel in an aquarium in the experimental facilities of Inge and Jan Boëtius at the Danish Institute for Fisheries and Marine Research, now DTU Aqua (photograph, Inge Boëtius, Jan Boëtius and Paul Juhlin)

information on the general behaviour of the eels while they were migrating. Indeed, data from some of these smaller, implanted tags confirm both the speed and the unique migration behaviour of eels. This research is continuing and information is being gleaned on the consistency of the eel migration pattern, the route and the speed.

Research on Eel Reproduction in Captivity

Schmidt's discovery of the Sargasso Sea as the spawning area of the European eel not only evoked broad interest in eel spawning migration and reproduction, but also interest in understanding the complex hormonal mechanisms that control eel maturation and spawning. Danish researchers Inge and Jan Boëtius (Fig. 3.17 top) participated in a number of expeditions to the Sargasso Sea exploring the spawning area, but it was their experimental work on the reproduction of eels in captivity that caught the attention of scientists internationally.

Inspired by the pioneering work of the French scientist Maurice Fontaine, who succeeded in inducing maturation in male and female eels by hormone injection (Fontaine 1936; Fontaine et al. 1964), many attempts were made in Europe in the second half of the nineteenth century to reproduce eels in captivity. In Denmark, the maturation process and production of gametes was the focus of much of this research (Bruun et al. 1949; Boëtius et al. 1962; Boëtius and Boëtius 1967). Inge and Jan Boëtius studied hormonally induced maturation and the spawning behaviour of ripe male and female eels in aquaria. They were the first to describe eel mating behaviour, which they documented photographically, and their photograph "Eels in love" (Fig. 3.17 bottom) has been redrawn and published numerous times to illustrate the mating of eels. Their experimental work led to the first *in vitro* fertilization of European eel eggs in 1977 (Boëtius and Boëtius 1980), which then stimulated further work that resulted in Russian scientists successfully hatching European eel larvae for the first time in the 1980s.

The pioneering work on eel reproduction described above forms the basis for today's research into methods of breeding eels for aquaculture. Eel farms of today still base their production on wild-caught glass eels, but the ever-decreasing number of European glass eels arriving on our shores, similar to the situation for other species of eel, encourages eel aquaculture to move away from wild-caught eels towards a self-sustaining culture in which offspring are produced from captive broodstock. In the past decade, researchers in Japan have made significant advances in captive reproduction of eel, developing methods and technology to produce viable larvae and glass eels (Tanaka et al. 2001; Kagawa et al. 2005), and recently their eels have completed a full life cycle in captivity (Ijiri et al. 2011). The achievements thus far are promising in terms of future commercial production of glass eels under controlled conditions in culture, and the subject is covered in more detail elsewhere in this book.

The Japanese achievements around 2000 (Aida et al. 2003) led to renewed research on European eel reproduction, and the development of a self-sustaining culture of eels based on glass eel production from captive broodstock became a goal of the EU. The main bottlenecks to the production of viable European eel larvae are similar to those of the Japanese eel. They include poor egg quality through hormonally induced maturation, limited fertilization success, and embryonic and larval development failure. From 2005 to 2008, however, a Danish research team aiming to reproduce European eels in captivity improved egg quality and fertilization rates, and viable eel larvae were produced

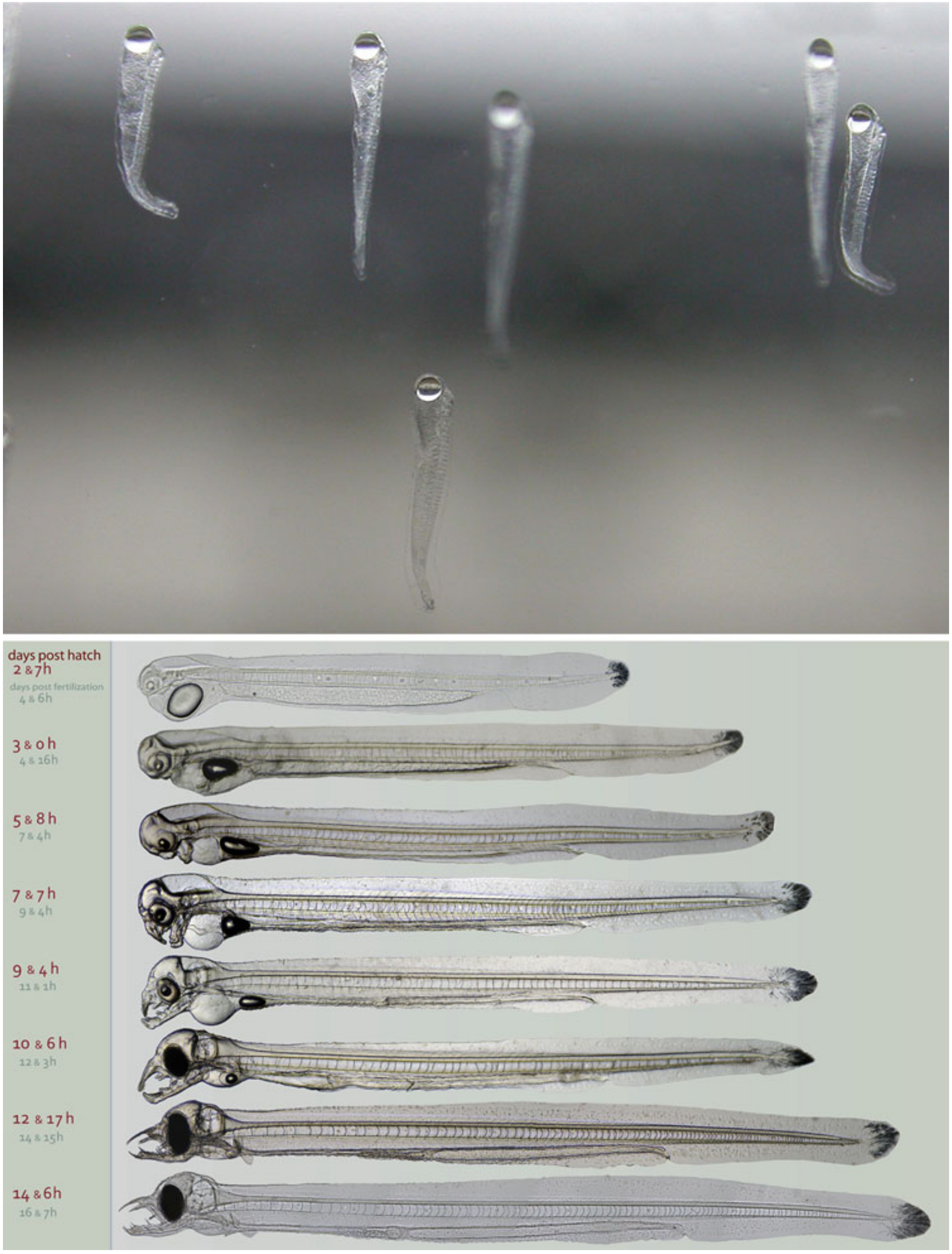

Fig. 3.18 *Top:* Newly hatched larvae of the European eel, the yolksac including a large oil droplet that helps a larva maintain neutral buoyancy. The bent newly hatched larvae straighten within a few hours (photograph, Sune Riis Sørensen, DTU Aqua). *Bottom:* Larval development in the European eel through the yolksac stage (0–12 days post-hatch) into the leptocephalus stage (14 day post-fertilization) in Danish experiments (photographs and graphics courtesy Jonna Tomkiewicz and Sune Riis Sørensen, DTU Aqua)

in large numbers (Fig. 3.18 top; Tomkiewicz and Jarlbæk 2008). The work led for the first time to European eel larvae completing their yolk-sac stage (pre-leptocephalus stage) in culture at an age of 12 days; during that stage, development depends exclusively on the nutrients deposited in the egg. More recently, in 2010, the same research team succeeded in culturing larvae in pilot feeding experiments, which then developed into the leptocephalus stage (Fig. 3.18 bottom; Tomkiewicz 2012). Currently, research on the reproduction of European eels is being fostered through the Danish-coordinated international research project PRO-EEL, which involves several leading research institutes and the aquaculture industry around Europe. A particular challenge now is to develop suitable feed for larvae and culture conditions appropriate for rearing leptocephali, a task that researchers in Japan continue to address in their efforts at developing a commercial production technology for Japanese glass eels.

Fig. 3.19 *Top:* Traditional eel dishes: (*left*) a Danish open sandwich ("smørrebrød") with smoked eel, omelette, tomato and chives on dark rye bread; (*right*) a more sophisticated, less-traditional way of serving smoked eel, with ice cream, oyster-filled tomato, parsley jelly, salmon roe and egg yolk (photographs, © Claes Bech-Poulsen, Kontrast ApS). *Bottom:* An eel feast at Tusenæs, Zealand, Denmark (photograph, Merete Ettrup)

Eels in Danish Culture and Society

Few fish are surrounded by as much mystery as eels. In many ways, eels do have some remarkable features. They can travel over land like snakes, their blood is poisonous, they migrate thousands of kilometres to spawn in the Sargasso Sea, and they have an uncanny, highly sensitive sense of smell. Likely because of some of these features, eels have been the subject of many sayings and myths over the years, but unlike the myths of some countries, whose myths suggest a more refined spiritual or religious leaning, Danish and other Scandinavian myths and sayings about eels often suggest a practical food-and-drink-related approach towards them. Some old sayings and myths heard in Denmark, along with some interesting suggestions for eel use in folk medicine are quoted below.

"If an eeler got an eel in the very first thrust, he might as well return home, since the yield would be poor. This seems lacking in logic, but fortunately the bad omen can be revoked by a drink; that is why one should always bring liquor when going eel fishing."

"The first caught eel of the autumn was not to be sold, but should be eaten by oneself, or one would have little luck catching eels the rest of the year."

"If a fisherman bit the head of his first eel, he would become 'King of eels', and eels would always seek him!"

"If you covered the rockers on a cradle with eel skin, the child could not be bewitched."

"Catholic priests who break the vow of celibacy will turn into eels after death."

"Drunkards can be treated with liquor in which eels had run themselves to death. The filtrated tincture should be drunk by the drunkard, who from then on would feel deep disgust for alcohol!"

"The sap of ash tree leaves mixed with eel fat and the juice of ant eggs can cure ear aches."

"Fresh eel can be eaten as a cure for constipation."

"Eel blood mixed with mint water can be drunk against colic."

"Eel skins can be placed on legs or joints to heal cramps."

Eels as Food

Eels are or rather were a traditional dish in Denmark. Because of their decline, however, few young people have grown up with eels as a common food, and it is mainly middle-aged and older people who like to eat eels. Eels are prepared and served in various ways. The traditional Danish ways to prepare eels were to salt large specimens of 1 kg or more, to smoke medium-sized eels of 350–1,000 g and to fry the smaller eels.

There are many different eel dishes in Denmark (two are shown in Fig. 3.19 top). Some of the more popular are fried eel with parsley sauce and potatoes, fried eel with stewed potatoes, smoked eel with eggs and wholemeal bread, eel soup, boiled eel with mustard sauce and potatoes, fried eel with stewed pear, fried eel with baked beetroot and apple, fried eel with herb cheese, and jellied eels. Typical herbs used in eel dishes are bay leaves, thyme, parsley, sage, tarragon, dill, chives and lots of pepper, but also garlic, curry powder and basil. Redcurrants and blueberries are a delicate topping sometimes used by top chefs.

Apart from individual dishes, eel feasts are traditional Scandinavian events, and they typically took place at the coast, where people used to support themselves by fishing for eels. They are feasts at which one can eat eel cooked in many different ways while consuming beer and schnapps (Fig. 3.19 bottom). The tradition of eel feasts began several hundred years ago, when the King owned all fishing rights and was willing to sell (for a royalty) those rights through local squires. Tradition had it that when the time was right and fishing for eels was at its most productive, the squires would arrive to collect the royalty, bringing potatoes and liquor, and the fishers would open their eel booths and offer the best of their fresh eels. One good story is that a true eel feast takes place when a group of men walks into an eel booth at dusk to eat and drink, then emerges from the booth in the early dawn with no recollection whatsoever of what had happened during the night! It is worth noting too that, because of local superstition or perhaps even morals, eel feasts used to be for men only, but nowadays both men and women participate in the festivities.

Final Comments

The eel was for eons one of the most important food fish in Denmark. However, its importance to the country and people is now dwindling simply as a consequence of declining abundance. Until the 1920s, the gear used to catch eels hardly changed and traditions did not alter, but since then, new gears, increasing fishing efficiency, the deterioration of eel habitats, barriers to both up- and downstream migration etc. have reduced the population and changed traditions. Focus in Denmark is now firmly on conservation of the stock, including finding means of sustainable exploitation and developing aquaculture.

Ongoing research into eel migration, reproduction, genetics and larval development is crucial to understanding the complexity of eel biology and hence managing these unique and fascinating fish. Equally important is to find means of preserving and improving habitats, and eliminating or at least lessening pollution and obstructions to up- and downstream migration. With successful reproduction of the European eel in captivity, the basis for self-sustained aquaculture will be laid, and in time too perhaps this can help improve the situation for the species in the wild.

As the European eel appears to consist of just one population, its future in Denmark is linked to the dynamics of the species Europe-wide and the ability of European people to work together to save it from extinction. Reinforcing this statement, ICES has stated that "The first priority is to get the message across to fishermen, managers, and politicians, that the most widespread and highest employing, single fish stock in Europe is dangerously close to collapse" (http://www.ices.dk/marineworld/eel.asp). The hope must therefore be that the EU Council Regulation of 2007 and national eel management plans will include measures sufficient to support the recovery of the European eel. Even if successful, however, any recovery will take a very long time.

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