The Sargasso Sea Subtropical Gyre
The Spawning and Larval Development Area of Both Freshwater and Marine Eels
Michael J. Miller and Reinhold Hanel

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Further details:

Dr David Freestone, Executive Director, Sargasso Sea Alliance, Suite 300, 1630 Connecticut Avenue NW, Washington D.C., 20009, USA.
Email: dfreestone@sargassoalliance.org

Kate K. Morrison, Deputy Director, at the same address
Email: kmorrison@sargassoalliance.org

The Secretariat of the Sargasso Sea Alliance is hosted by the Washington D.C. Office of the International Union for the Conservation of Nature (IUCN).

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COVER PHOTO: European eel, Reinhold Hanel.
The Sargasso Sea Subtropical Gyre
The Spawning and Larval Development Area of Both Freshwater and Marine Eels

Michael J. Miller
Research Scientist
Atmosphere and Ocean Research Institute
The University of Tokyo
Chiba, Japan

Reinhold Hanel
Director
Thünen-Institute of Fisheries Ecology
Hamburg, Germany
FOREWORD

Between 2010 and 2012, a large number of authors from seven different countries and 26 separate organisations developed a scientific case to establish the global importance of the Sargasso Sea. A summary of this international study was published in 2012 as the “Summary science and Supporting Evidence Case.” Nine reasons why the Sargasso Sea is important are identified in the summary. Compiling the science and evidence for this case was a significant undertaking and during that process a number of reports were specially commissioned by the Sargasso Sea Alliance to summarise our knowledge of various aspects of the Sargasso Sea.

This report is one of these commissioned reports. These are now being made available in the Sargasso Sea Alliance Science Series to provide further details of the research and evidence used in the compilation of the summary case. A full list of the reports in this series can be found in the inside back cover of this report. All of them can be downloaded from www.sargassoalliance.org.

Professor Howard Roe
Science Advisory Committee Chair
Sargasso Sea Alliance

Professor Dan Laffoley
Science Coordinator
Sargasso Sea Alliance
The Sargasso Sea Subtropical Gyre: The Spawning and Larval Development Area of Both Freshwater and Marine Eels

The Sargasso Sea is a large oceanic region that makes up the western portion of the subtropical gyre of the North Atlantic and is perhaps most famous among scientists for being the spawning area of the two species of freshwater eels, the European eel, *Anguilla anguilla*, and the American eel, *Anguilla rostrata*. How and where these eels reproduce was a mystery since the age of the Greek philosopher Aristotle, because the eels would leave freshwater never to be seen again, except that their offspring, called glass eels would mysteriously return again every year. Eventually though, their larvae were identified and by gradually searching for smaller and smaller larvae of these eels in the ocean, which are called leptocephali, by using a variety of ships to collect data, the Danish scientist Johannes Schmidt finally discovered that these two species of eels actually migrate all the way from their freshwater and estuarine growth habitats in Europe and North Africa and eastern North America, to the southern region of the Sargasso Sea to spawn (Schmidt 1912, 1922; Figure 1, 2). This discovery was considered one of the

**Figure 1.** Map showing the general regions where different sizes of Atlantic anguillid eel leptocephali were collected by Johannes Schmidt in the Sargasso Sea region, for the American eel, *Anguilla rostrata* (dashed lines), and the European eel, *Anguilla anguilla* (solid lines). Modified from Schmidt (1922).

**Figure 2.** Johannes Schmidt led the effort to discover the spawning areas of the Atlantic anguillid eels in the Sargasso Sea during the early part of the last century using the three ships shown here as well as other ships including commercial vessels that were used as “ships of opportunity”. This enabled him to sample for leptocephali in more areas and at different times of year, without having to use his own ships all the time (modified from Schmidt 1925, Bertin 1956 and Sinclair 2010).
great discoveries in fish biology, and their migration to spawn in the Sargasso Sea is still one of the classical examples of animal migration.

However, all is not well with these eels despite their spawning area being located offshore in the Sargasso Sea far away from most human influences. The population levels of both species have declined, and recruitment to many areas has fallen drastically in the last 3 decades. For the American eel, recruitment to the northern edge of its range at the St. Laurence River in Canada has fallen drastically (Casselman 2003), and recruitment of the European eel to much of its range has fallen so low that since 2009 it has been listed on the Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

As a result of the steep decline in European eel numbers, the European Commission has proposed and implemented a Community Action Plan for protection and recovery of the severely depleted eel stock (Council Regulation (EC) No 1100/2007). This regulation includes the preparation of management plans for each eel river basin by the member states with the objective to reduce anthropogenic mortalities to permit the escapement to the sea of at least 40% of the silver eel biomass relative to the best estimate of escapement that would have existed without anthropogenic influences. It is hoped that by taking discrete management actions for each EU river basin, the number of spawners reaching the Sargasso Sea can be increased.

There has been much debate and concern about what has caused the decline of the Atlantic eels (e.g. Dekker et al., 2003; ICES 2001, 2006, 2007), with explanations ranging from habitat loss and overfishing, or parasites, virus infections and contaminants accumulating in their bodies affecting the migration or spawning abilities (e.g. Robinet and Feunteun 2002; Kirk 2003; van Ginneken et al., 2005; Palstra et al., 2007; Belpaire and Goemans 2007; Jakob et al., 2009a,b), to changes in the physical or biological characteristics in their Sargasso Sea spawning area or during their long larval migrations back to their continental growth habitats (Castonguay et al., 1994; Knights 2003). For example, the implementation of dams in both Europe and North America has reduced the amount of effective habitat for diadromous species greatly, and what river habitat that was left available for recruitment and safe outmigration of the adults was heavily impacted by development and pollution (Haro et al., 2000). Fishing pressure on the recruiting glass eel stage also increased in recent decades due to the export trade for aquaculture in Asia. Compounding these factors, at about the same time as the large declines began, there was a major regime shift in the North Atlantic that altered some physical and biological characteristics in the Sargasso Sea and the wider ocean basin, thus possibly influencing the survival or transport of their leptocephali (Castonguay et al., 1994; Knights 2003; Friedland et al., 2007; Bonhommeau et al., 2008a,b; Kettle et al., 2008; Miller et al., 2009; Durif et al., 2011).

Regardless of what is causing the declines in these eel species, what is known is that they both appear to spawn in the southern part of the Sargasso Sea. This spawning area was discovered in the early part of the 20th Century after collections of leptocephali were made in many regions of the Atlantic Ocean and Mediterranean Sea, but small larvae were only found in the southern Sargasso Sea (FIGURE 1, Schmidt 1912, 1922). The Sargasso Sea subtropical recirculation gyre (Marchese and Gordon 1996; Marchese 1999) has the northward flowing Florida Current to the west that continues as the Gulf Stream to the north, with westward flow along the southern margin of the gyre as shown diagrammatically in FIGURE 3 (Worthington 1976; Stommel et al., 1978; Schmitz and McCartney 1993). The smallest larva
were found in the southern Sargasso Sea where there is westward flow that can transport their leptocephali towards the Florida Current. The detailed location of the spawning area was documented by collecting small recently hatched leptocephali 4–7 mm during a variety of scientific sampling surveys by Danish, German, and American scientists in the early (Schmidt 1922) and latter parts of the last century (e.g. Schoth and Tesch 1982; McCleave et al., 1987; Kleckner and McCleave 1988). The later cruises and analyses of catch data that occurred after the time of Schmidt’s research showed that the more recently spawned larvae < 10 mm were widely distributed in overlapping areas south of about 30°N (FIGURE 4), with the European eel spawning slightly to the east of the American eel. Many stations collected small recently spawned larvae of both species (McCleave et al., 1987), indicating that their spawning areas were overlapped as illustrated by the red squares in FIGURE 4.

During the later part of the last century, it was also shown that spawning was occurring south of distinct temperature fronts (FIGURE 5) that are consistently present in the Sargasso Sea during the spawning season in late winter and early spring (Kleckner and McCleave 1988) and this was confirmed again more recently (Munk et al., 2010). These fronts were also found to cause discontinuities in the assemblages of anguillid and other

**FIGURE 4.** Map showing the overlapping spawning areas of the two Atlantic eel species based on the distributions of their small leptocephali (10 mm) with 2 blue shaded ovals, and stations where small recently hatched larvae 7 mm or smaller of both species were collected together (red squares). Map was adapted from McCleave et al., (1987). Major currents such as the Gulf Stream, Antilles Current and the North Equatorial Current (NEC) are shown.

**FIGURE 5.** Cross section of a front in the Sargasso Sea showing the contrast in temperature on the south side (right) and north side (left). This front was found to have an eastward frontal jet current with maximum velocities of 50 cm/sec (see FIGURE 7). From Ericksen et al., (1991). Pressure is equal to depth in meters on the vertical axis.
leptocephali of various marine eel families (Figure 6) and the associated frontal jets, or countercurrents (Figure 7), appear to transport some leptocephali eastward (Miller and McCleave 1994). Water converges from both sides into these fronts causing strong eastward counter-currents to form (Mied et al., 1986; Eriksen et al., 1991; Weller et al., 1991; Pollard and Regier 1992).

Therefore, the Atlantic eels spawn in the middle of a complex area that includes oceanic fronts and strong countercurrents. Due to the atmospheric and oceanographic conditions that exist in that part of the Sargasso Sea, this region is called the Subtropical Convergence Zone, because it is where warm and cold water masses meet in the fall, winter, and spring. Transects made across these fronts showed their structure and the distribution and size of the anguillid leptocephali in the frontal zones (Kleckner

**Figure 6.** (A) Map showing most of the stations (Tesch and Wegner (1990) not shown) and transects of stations that were sampled in the spawning areas of the two Atlantic eels by American and German scientists between 1979 and 1989. Stations made by J. D. McCleave are shown by triangles for 1981, and transect lines for 1983 and 1985, and circles show the stations made by F. W. Tesch (in 1979). From Miller (1995). (B) Catch rate of the two species of Anguilla leptocephali collected in the 85E transect across the northern front in March 1985 are shown in red in (A). The shaded area shows the distribution of Southern Sargasso Sea Surface water up to the northern front. From Miller and McCleave (1994).

**Figure 7.** Plan view of a front with a strong frontal jet, showing the water density contrast in the front plotted at a depth of 50 m (density 25.2-25.6) on 20 February 1986 in the left panel. Thin lines show the cruise track of the ship that was surveying the front. The right panel shows the Acoustic Doppler Profiler water velocities across the front, with a frontal jet seen in the right side of the survey area where the front was most distinct. From Pollard and Regier (1990).
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and McCleave 1988). Similar size ranges of leptocephali of both species were collected in most areas (e.g. FIGURE 8). The 1979 German survey in the Sargasso Sea showed that spawning can occur over a wide longitudinal zone resulting in small leptocephali being widely distributed (Schoth and Tesch 1982) (FIGURE 9).

The eels seem to have evolved the ability to detect the location of this area and appear to spawn within a narrow band of latitude between the fronts (Kleckner and McCleave 1988; Miller and McCleave 1994; Munk et al., 2010). For example, if the migrating eels can detect when they have crossed a frontal region, they may stop migrating and begin to look for mates and prepare for spawning (McCleave 1985, 1987). However, eels also have a magnetic sense (e.g. Nishi et al., 2004, 2005), as do some other marine animals (Lohmann et al., 2008), which could be used to imprint on the geomagnetic location where they were born and then return back there. This could help guide them directly to their spawning areas and then fronts and ocean currents could then influence their final spawning location. Anguillid eels in the western North Pacific appear to use a long seamount chain, the West Mariana Ridge to the west of Guam, as a landmark defining their spawning area (Tsukamoto 2006; Tsukamoto 2011), but there are no seamounts in the Atlantic eel spawning area, so the oceanic fronts may serve as alternative landmarks.

After the spawning season that extends from about February to June, the leptocephali of both anguillid species appear to become widely distributed as they are transported by the currents and eddies in the region (Boetius and Harding 1985; Kleckner and McCleave

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**FIGURE 8.** Size of both species of anguillid leptocephali collected in a frontal zone in the Sargasso Sea during February 1983 by Kleckner and McCleave (1988).

**FIGURE 9.** Catches of *Anguilla* leptocephali < 10 mm in size in the Sargasso Sea in March and April 1979, showing the overlap between the two species in the west and the predominance of European eel larvae in the east. From Schoth and Tesch (1982).
flow of the Antilles Current to northeast of the northern Bahamas that flows into the Florida Current. American eel leptocephali must then cross the Florida Current and Gulf Stream to recruit to the east coast of North America, but those of the European eel must continue being transported to the east by the Gulf Stream and North Atlantic Drift. The actual pathway and transport time of European eel leptocephali remains poorly understood however, due to the limited spatial and temporal coverage of sampling surveys across the eastern part of the basin and difficulty in determining the age of the larvae after they reach Europe (McCleave et al., 1998; McCleave 2008; Bonhommeau et al., 2010).

Studies of larval distribution and modeling of larval
drift patterns suggest that most European eel leptocephali probably use the Gulf Stream-North Atlantic Drift after moving west through the southern Sargasso (McCleave and Kleckner 1987; Kettle and Haines 2006; Bonhommeau et al., 2009). However, direct eastward or northeastward movement of some leptocephali appears to be a possible second route (Miller et al., 2009) as also discussed recently (Munk et al., 2010), due to flows associated with the frontal jets that form in the Subtropical Convergence Zone each year (Miller and McCleave 1994; Ullman et al., 2007). Regardless of how they achieve it, or how long it takes, the migration of the European eel is probably the longest of any anguillid species, making its recruitment especially vulnerable to oceanic changes.

One problem in understanding if changes in the ocean are affecting the recruitment patterns of anguillid eels originating from the Sargasso Sea, is that little is known about the biology of their leptocephali. Unlike most fish larvae, leptocephali appear to feed almost exclusively on particulate organic material such as “marine snow” and discarded larvacean houses (Otake et al., 1993; Mochioka and Iwamizu 1996), but not on zooplankton like most fish larvae (Miller 2009). Marine snow can contain a variety of materials from various types of marine organisms though (Alldredge and Sliver 1988; Shanks and Walters 1997; Kiørboe 2000), as was also suggested by a recent barcoding study on the diet of anguillid leptocephali in the Sargasso Sea (Riemann et al., 2010). Anguillid leptocephali have long-thin and forward pointing teeth (FIGURE 13) that are well-shaped for grasping and compressing particulate materials to be swallowed. There has only been one study on the growth of anguillid larvae (Castonguay 1987) though...
(Figure 14), so much remains to be learned about their biology. It is known, that anguillid leptocephali live in the upper few hundred meters of the ocean, with larger sizes being found in the upper 100 m at night and deeper during the day (Castonguay and McCleave 1987; Miller 2009) (Figure 15).

Although the Sargasso Sea is famous for being the spawning area of the anguillid eels as described so far, it is also known to be the spawning area of at least one species of congrid eel. The first realization that some marine eels make long offshore migrations also resulted from the early surveys in the Sargasso Sea, when Schmidt (1931) reported finding the small leptocephali of conger eels offshore. He proposed that C. oceanicus, and the European conger eel, Conger conger, also migrated to spawn in the Sargasso Sea. However, more recent larval collections in the Sargasso Sea found that only leptocephali of the American conger eel, C. oceanicus,

**Figure 14.** Ages (no. of increments) and growth pattern of anguillid leptocephali from the Sargasso Sea (left) estimated from their otolith microstructure (right). From Castonguay (1987).

**Figure 15.** Depth distribution of anguillid leptocephali that were collected in the Sargasso Sea during spring, summer, and fall of 1983–1985 using a 2-m ring net during both day (white bars) and night (black bars) in the study of Castonguay and McCleave (1987). As the larvae get larger they show increasing evidence of vertical migration from shallow layers at night to deeper layers during the day.
were present there along with those of a local tropical conger species, but not those of *C. conger* (McCleave and Miller 1994). The confirmation that *C. oceanicus* migrates offshore from North America to spawn in an overlapping area with *A. rostrata* (Figure 16), showed that two eel genera had evolved long offshore spawning migrations for reproduction in the North Atlantic. After spawning offshore in the southwest Sargasso Sea, like *A. rostrata*, the larvae of *C. oceanicus* would then drift westward and cross the Florida before swimming over the continental shelf to where its larvae enter coastal waters and metamorphose into young eels that live in marine habitats (Bell et al., 2003). This situation is even more interesting now, since the most abundant commercial fisheries species of conger eel, *Conger myriaster* of East Asia, was also recently discovered to migrate offshore to spawn in an analogous location in the western North Pacific as that of the American conger eel (Miller et al., 2011). The fact that both anguillids and conger eels in each of the northern hemisphere subtropical gyres migrate to spawn offshore suggests convergent evolution of migration strategies has occurred in these species (Miller et al., 2011).

There is also another congrid species that uses the Sargasso Sea for spawning and larval growth, and there are several species of mesopelagic eels that spawn there too. The bandtooth conger, *Ariosoma balearicum*, appears to make a shorter spawning migration to spawn offshore along the eastern edge of the Florida Current and the western edge of the Sargasso Sea (Miller 2002). By spawning in this location, its leptocephali then become widely distributed throughout the Sargasso Sea gyre both north and south of the frontal zone, which is in contrast to the anguillid and conger leptocephali, which only use the southern part of the gyre. In fact, *A. balearicum* leptocephali are one of the most abundant leptocephali in the February to April season where they are consistently present at a very narrow size range.

**FIGURE 16.** General locations of the offshore spawning areas of freshwater eels and conger eels (ovals). a, b Anguillid eels (from McCleave et al., 1987; Kuroki et al., 2009; Tsukamoto et al., 2011). c, d Marine eels of the genus *Conger* (from McCleave and Miller 1994; Miller et al., 2011). Both types of eels spawn within westward currents and their larvae enter western boundary currents (Gulf Stream, Kuroshio) that transport them northward in each geographic range. Some larvae also move west and south to other parts of their species ranges that are shown with colored lines on coastlines or shading (inland ranges of freshwater eels are not shown). From Miller et al., (2011).
(FIGURE 17) after their spawning season in the fall (Miller 2002). The other eels that spawn far offshore in the Sargasso Sea are the mesopelagic species of the families Eurypharyngidae, Nemichthyidae, and Serrivomeridae (Miller and McCleave 1994, 2007; Miller et al., 2006). The newly spawned larvae of these three families are consistently present in the February to April season.

These eels live completely pelagic lives in the midwater zone of the ocean at depths of about 200 to 2000 m, but their leptocephali all live in the surface layer and mix with those of anguillid eels and other species (Miller and Tsukamoto 2004). Actually, anguillid eels are most closely related to these particular pelagic eels (Inoue et al., 2011), which means that the open ocean spawning behavior of freshwater eels has been retained from their ancestors that lived in the deep ocean. In the Sargasso Sea, the small leptocephali of *Nemichthys scolopaceus* are one of the more abundant larvae offshore during the anguillid spawning season (FIGURE 17). Other rare deep-sea pelagic eels that are very poorly known such as the Cyematidae frequently spawn in the Sargasso Sea as well (Smith and Miller 1996). The leptocephali of nemichthyids, and also those of derichthyids that mostly spawn after April, are abundant across the Sargasso Sea in the summer and fall seasons along with anguillids (Castonguay and McCleave 1987b; Wipplehauser et al., 1996). After the larvae of these pelagic eels grow to full size, they then metamorphose into juvenile eels and move to deeper depths for feeding and growth.

This overview of the Sargasso Sea as a spawning area of eels has shown that this subtropical gyre is of critical importance to many eel species, which in turn are important ecological components not only in the Sargasso Sea itself, but in the other regions where their larvae eventually recruit. The American eels originating in the Sargasso Sea enter estuaries, rivers and lakes along the entire eastern and southern coastlines of the United States, and much of the east coast of Canada. The European eels recruit to western Europe, its Mediterranean coast and to North Africa. The congrid eels that spawn in the Sargasso Sea recruit to the US East Coast. Many mesopelagic eels also spawn in the Sargasso Sea and then recruit to its deeper depths. Therefore the Sargasso Sea is an important location for the spawning and larval development of eels, whose health and well being can have significant effects on many aquatic environments around the North Atlantic Ocean basin through the eels that eventually recruit there.

All regions of the worlds tropical and subtropical seas have marine eel faunas and leptocephali along their edges (Wouthuyzen et al., 2005; Richardson et al., 2004; Miller et al., 2002, 2006), mesopelagic eels in their deep waters, and a wide array of midwater fishes, crustaceans

![Figure 17](image_url)

**FIGURE 17.** Length frequency distributions of (A) *Nemichthys scolopaceus* and (B) *Ariosoma balearicum* leptocephali, collected in the seven transects across the frontal zone that are shown in FIGURE 6A, that were made in the February to April season. *N. scolopaceus* is a mesopelagic eel that spawns in the frontal zone of the Sargasso Sea, and *A. balearicum* migrates offshore into the western Sargasso Sea to spawn, with their larvae using the Sargasso Sea gyre as a larval development area. From Miller and McCleave (1994).
and other planktonic organisms like those present in and adjacent to the Sargasso Sea (Backus et al., 1969; Miller and McCleave 1994, 2007; Ross et al., 2007; Bucklin et al., 2010; Sutton et al., 2010); but none are the spawning area of a species of anguillid eel that actually must return back eastward thousands of kilometers from where it was born, like the European eel. All other anguillid species simply rely on westward and then north or south transport to their recruitment areas by ocean currents (Tsukamoto et al., 2002; Miller 2003, 2009; Aoyama 2009) or spawn locally after short distance spawning migrations (Aoyama et al., 2003). The long migration of the European eel to and from the Sargasso Sea seems to have put it in a precarious position, with a host of problems caused by human impacts, ocean-atmosphere changes, or even possibly global warming that have its population size reduced to critical levels.

Although the Sargasso Sea is seemingly becoming newly famous as the spawning area of the only anguillid eel possibly threatened with near-extinction, it also has other unusual animals and a unique geographic setting, with the massive shallow banks of the Northern Bahamas in the southwest and the small shallow banks of Bermuda in the north (FIGURE 18). The western North Pacific has a similar subtropical gyre with eel spawning areas, but with no massive banks or far offshore banks like Bermuda. The Sargasso Sea is located at a higher latitude and is a more self contained gyre, without major branching currents along its southern margin (FIGURE 16).

The Sargasso Sea is also a place where natural selection has produced some interesting species adapted to live exclusively within the floating communities of sargassum weed that drifts around the spawning area of eels, such as the shrimp and fish shown in FIGURE 18. The various interesting geographic features of the Sargasso Sea and the many creatures found there, in combination with its unique pattern of distinct frontal bands that form in the colder months of the year, make this region a unique part of the world’s oceans not only for eels, but for all creatures of the sea, which calls for the need to carefully protect this special place on earth.
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