EDDIES

See **MEDDIES AND SUB-SURFACE EDDIES; MESOSCALE EDDIES**

EELS

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Introduction

Migratory, catadromous eels of the genus *Anguilla* have among the most fascinating life cycles of all fishes. Catadromous fishes breed in the ocean but feed and grow in fresh waters or estuaries. This cycle includes a larval or juvenile migration from breeding to feeding area and an adult migration back. These two migrations have been termed denatant and contranatant to imply that the larval migration is accomplished largely by drift with currents and the adult migration by swimming against the currents. These terms get the essence of eel migration, but they fail to capture the complexity and mystery of eel migrations. Anguillid eels are sexually, ecologically, and behaviorally highly adaptive. They occur naturally in a greater diversity of habitats than any other fishes. These statements apply mainly to the feeding and growth stages in continental waters. In contrast, successful spawning and larval survival seems to depend on rather specific oceanic conditions for all *Anguilla*.

Juveniles and adults of *Anguilla* are elongate, rather cylindrical, darkly pigmented fishes, reaching about 30 cm to nearly 200 cm at maturity depending on species and gender. They have long continuous median fins extending from the anus around the tail and well forward on the back. The contrast with the larvae, termed leptocephali, is extreme. Leptocephali are laterally compressed and deep bodied. They are nearly transparent, with pigment restricted to the retina of the eye. A major metamorphosis occurs between larva and juvenile.

This article considers eels of the Family Anguillidae, which is one of about 22 families of eels. Eels are primitive bony fishes. Within the bony fishes (Class Osteichthyes), there are two orders of eels. The Anguilliformes contains 15 families, including spaghetti eels, morays, cutthroat eels, worm eels, snipe eels, and conger eels. The Saccopharyngiformes contains seven families, including deep-sea gulper eels. These two orders are unified by the presence of leptocephali with continuous dorsal, caudal, and anal fins. W. Hulet and R. Robins have argued that the evolution of the leptocephalus, which is in ionic equilibrium with, and nearly isosmotic with sea water, in these primitive fishes was one solution allowing fishes to complete their life cycle in the sea.

Only species in the genus *Anguilla* are truly catadromous, though not all individuals enter fresh water. The other families are marine, ranging from abyssalpelagic to epipelagic to coastal, with juveniles of some species being estuarine. The easily viewed stages in the life cycle of *Anguilla* occur in fresh water, and they are the only group of eels to enter fresh waters, so they are often called freshwater eels, an unfortunate name, given their extensive migrations at sea.

Taxonomic and Geographic Diversity of *Anguilla*

Fifteen species of *Anguilla* comprise the Anguillidae (**Table 1**). These can be grouped into tropical and temperate species on the basis of coastal and freshwater distribution, and of proximity of those distributions in continental waters to the spawning areas. Two temperate species occur in the North Atlantic Ocean, one in the North Pacific, and two in the South Pacific. Eight tropical species are all distributed in the western Pacific and Indian Oceans. Two species extend from the tropics into temperate zones, one in the South Pacific and one in the Indian Ocean.

All species require warm, saline, offshore water for successful reproduction. Appropriate currents must be present to transport the larvae toward continental waters. The widely distributed, temperate species use anticyclonic, subtropical gyres for spawning and use associated western boundary currents for distribution of larvae. The European eel

Table 1 Taxonomic diversity and continental distribution of the Family Anguillidae with its single genus Anguilla, 15 species and four subspecies

Scientific name	*English common name*	*Continental distribution*
A. anguilla (Linnaeus, 1758)	European eel	(Te)[a] Iceland, Europe and North Africa from Norway to Morocco, Mediterranean basin to Black Sea, Canary Islands, Azores
A. australis[b] Richardson, 1841	Shortfin eel	(Te) Lord Howe Island, east coast of Australia, Tasmania, New Zealand, and Auckland, Chatham, and Norfolk Islands, New Caledonia
A. bengalensis bengalensis (Gray, 1831)	Indian mottled eel	(Tr) India, Sri Lanka, Myanmar, Andaman Islands, northern Sumatra
A. bengalensis labiata (Peters, 1852)	African mottled eel	(Tr) Eastern Africa from Kenya to South Africa
A. bicolor bicolor McClelland, 1844	Indonesian shortfin eel	(Tr) Eastern Africa, Madagascar, India, Myanmar, Sumatra, Java, Timor, north-western Australia
A. bicolor pacifica Schmidt, 1928	—	(Tr) Eastern Indonesia, New Guinea, Taiwan
A. celebesensis Kaup, 1856	Celebes longfin eel	(Tr) Sumatra, Java, Timor, the Philippines, Celebes, western New Guinea, smaller islands of eastern Indonesia
A. dieffenbachii Gray, 1842	New Zealand longfin eel	(Te) New Zealand, and Auckland and Chatham Islands
A. interioris Whitley, 1938	New Guinea eel	(Tr) Eastern New Guinea
A. japonica Temminck and Schlegel, 1846	Japanese eel	(Te) Northern Vietnam, northern Philippines, Taiwan, China, Korea, and Japan
A. malgumora Popta, 1924	—	(Tr) Eastern Borneo
A. marmorata Quoy and Gaimard, 1824	Giant mottled eel	(Tr) South Africa, Madagascar, Indonesia, the Philippines, Japan, southern China, Taiwan, eastward through Pacific islands to the Marquesas
A. megastoma Kaup, 1856	Polynesian longfin eel	(Tr) Solomon Islands and New Caledonia eastward to Pitcairn Island
A. mossambica (Peters, 1852)	African longfin eel	(Tr–Te) Eastern Africa from Kenya to South Africa, Madagascar, Mascarenes
A. obscura Günther, 1871	South Pacific eel	(Tr) New Guinea to the Society Islands
A. reinhardtii Steindachner, 1867	Speckled longfin eel	(Te–Tr) Australia from Victoria to Cape York (north tip), New Caledonia, Lord Howe Island
A. rostrata (Lesueur, 1817)	American eel	(Te) Southern Greenland, eastern North America from Labrador through the Gulf of Mexico and the West Indies to Venezuela and Guyana, Bermuda

[a] Te, temperate species; Tr, tropical species.

[b] Australian and New Zealand subspecies are sometimes recognized.

is unusual in having its continental distribution on the eastern side of an ocean basin.

Life Cycle

Life cycles are best known for the temperate species, but they are undoubtedly similar for the tropical species (**Figure 1**).

Spawning Areas and Times

Spawning of adult eels has never been observed in nature. Spawning areas and times are inferred from the distribution of small leptocephali. A fascinating case was the discovery of the spawning area of the European eel by Danish fishery biologist, J. Schmidt. When Schmidt in 1904 caught a 7.5-cm long leptocephalus of the European eel west of the Faroes in the north-eastern Atlantic Ocean, the chase was on. Between 1913 and 1922, Schmidt made four research cruises in the North Atlantic, and commercial vessels collected plankton samples for him. Only in the western North Atlantic were European leptocephali less than 1 cm long captured, in an area 20–30°N and 50–65°W. Larger leptocephali were found to the north and east across the Atlantic toward Europe. Schmidt also caught a few small American eel leptocephali west of the locus of small European leptocephali.

Recent research by F.-W. Tesch in Germany and at the University of Maine has confirmed that the

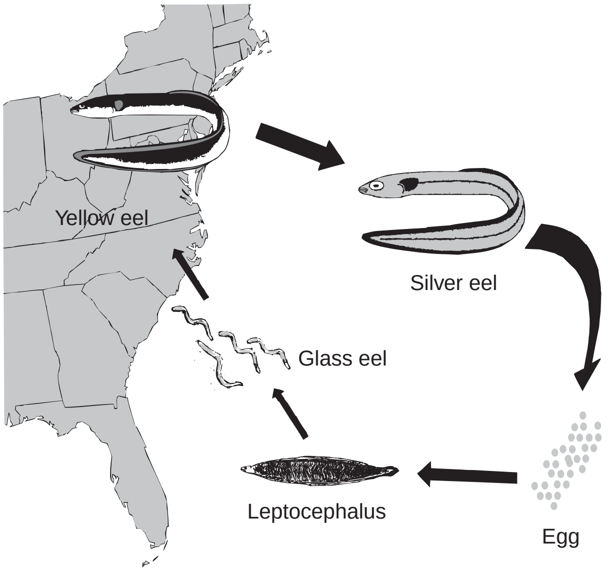

Figure 1 Catadromous life cycle of a temperate species of *Anguilla*, exemplified here by the American eel, *A. rostrata*.

south-western portion of the North Atlantic, the Sargasso Sea, is a primary spawning area for both Atlantic *Anguilla*. From the distribution in space and time of leptocephali less than 1 cm long, the European eel spawns from February through June, primarily March and April, at about 50–75°W in a narrow zonal band. The American eel spawns from February through April, at about 53–78°W. The two species overlap in space and time. The northern limit to spawning seems to be near-surface frontal zones in the subtropical convergence, which may serve as a cue for the adults to cease migrating and to spawn. Not all areas of the North Atlantic, especially south of 20°N, have been adequately sampled to rule out other spawning areas.

Small leptocephali of the Japanese eel have been collected in July in a salinity frontal zone at the northern edge of the North Equatorial Current between 131° and 147°E, west of the Mariana Islands in the western North Pacific. Spawning areas for the Australian and New Zealand temperate species and for most of the tropical species are speculative. Spawning areas of some tropical species may not be far offshore of the areas of continental distribution.

Eggs

In the sea, eggs are presumed to be broadcast into the plankton and fertilized externally. Mature eggs of American, European, and Japanese eels, obtained by hormone injections of females, are transparent and about 1 mm in diameter. Eggs of the Japanese eel hatch in 38–45 h at 23°C. Japanese leptocephali are about 2.9 mm long at hatching.

Leptocephali

Leptocephali of *Anguilla* are part of the epipelagic plankton. Their bodies are transparent and laterally compressed, with body height being about 20% of length. A series of W-shaped myomeres (muscle segments) extends from head to tail. Inside the myomeres is an acellular, mucus-like matrix. The myomeres are overlain by a thin epithelium. The head is small (leptocephalus means slender head) and bears a set of fang-like teeth projecting forward. Eyes and olfactory organs are well developed. Dorsal, caudal, and anal fins are continuous around the posterior of the body. Small pectoral fins are present. Leptocephali of *Anguilla* sp. are separated from one another primarily by the number of myomeres, e.g. 103–111 for the American eel and 112–119 for the European eel.

The mode of nutrition is in debate. Most workers have reported the absence of food in the simple guts of leptocephali, but the ingestion of bacteria, microzooplankton, or gelatinous organisms might go undetected. E. Pfeiler proposed that leptocephali absorb dissolved organic matter from the sea water across their epithelium. N. Mochioka and T. Otake showed that guts of leptocephali other than *Anguilla* collected at sea do contain larvacean houses, zooplankton fecal pellets, and detrital aggregates (particulate organic matter). Leptocephali may absorb dissolved organic matter across the gut.

Larval life lasts from a few months for the tropical species to debatably less than one to more than two years for the European eel. Estimates of larval duration are based on counting putative daily rings in otoliths (ear stones), but otoliths as indicators of age in days have not been validated. Leptocephali of the temperate species grow to about 6–8 cm, whereas those of the tropical species grow to 5–6 cm. Concurrently, leptocephali are gradually transported toward continental waters.

Glass Eels

At some time, a dramatic metamorphosis of form and physiology occurs. The body loses height and becomes rounder in cross-section, the larval teeth are resorbed, and the mucus matrix is catabolized. Newly transformed eels, still lacking pigment, are termed glass eels. Initially, they are still pelagic, and they move across the wide or narrow continental shelf into coastal waters. Along the way, they lose their strict pelagic habit and move on and off the bottom. Glass eels entering coastal waters and estuaries may become resident there, or they may continue into fresh waters. The invasion of estuaries and fresh waters is seasonal in the temperate species. At a particular location, the immigration usually peaks over two months, earlier at lower latitudes than at higher latitudes. For the Japanese and American eels and the two New Zealand species, glass eel immigration is in late winter, spring, and early summer. Immigration occurs throughout the year in some tropical species.

Elvers and Yellow Eels

Pigmentation develops rapidly after entry into estuarine or fresh waters, and the eels are known as elvers and then yellow eels. Elver refers loosely to small pigmented eels. Yellow eels are named because their ventral surfaces are yellow to white. The dorsal surfaces are usually shades of green to brown, plain or mottled depending on species. Yellow eels are in the juvenile growth phase of life.

Plasticity and adaptation

Habitat selection Gradual upstream movement of a segment of the yellow eel population occurs for several years, so older yellow eels become distributed from coastal waters to far inland. Eels occur in various habitats including saline coastal waters, estuaries, marshes, large rivers, small streams, lakes, ponds, and even subterranean springs. They occur in highly productive to highly unproductive waters. Temperate species invade waters with near tropical temperatures and waters that are seasonally ice covered.

Diet Yellow eels are opportunistic, consuming nearly any live prey that can be captured. Benthic invertebrates predominate in the diets, but fish, including eels, become important to larger eels. Eels respond to local abundances of appropriately sized prey through the seasons. Insect larvae may predominate in early summer and young-of-the-year fishes in late summer. Yellow eels are nocturnal, feeding mostly during the early hours of the night.

Sex determination and differentiation Sex is partially or wholly determined by environmental conditions. There are no morphologically differentiated sex chromosomes. Differentiation of the gonads does not occur until the yellow eel phase, with considerable variation in age size at differentiation. For American and European eels, a high population density of small eels seems to result in a high proportion of males and vice versa. Within a river basin, lakes generally have a higher proportion of females than riverine sections, which may reflect a population density or productivity effect.

Earlier hypotheses that there was a cline of increasing proportion of female American eels with increasing latitude, and that this was due to longer larval life of females, are not supported by current knowledge. Male-dominated rivers occur in northern as well as southern latitudes, and widely varying sex ratios occur in neighboring rivers. This is indicative of some mechanism for sex determination that acts at the river or habitat level.

Growth rate and sexual dimorphism Growth rate varies with length of the growing season and with productivity of the habitat. Growth rate also varies among individuals in the same habitat. For a given age, growth rate is greater for females than males, and females attain greater size at maturity than males. Annual growth rate decreases with age. Because the average age at maturity of females is greater than males, the annual average growth rate to maturity may sometimes be greater for males than females.

Determination of age of eels is by counting annual growth rings in the otoliths, but preparation of otoliths has varied among investigators. Accuracy and precision are low, with a tendency to overestimate the age of young eels and underestimate the age of older eels. Therefore, calculated growth rates must be interpreted cautiously.

Size and age at maturity Within a species and gender, size is more characteristic than age for when a yellow eel will metamorphose into a silver eel and migrate to sea (**Table 2**).

Studies of ages and sizes at migration of the European eel at 44 sites from Tunisia to Sweden allows generalization. Faster-growing eels of both sexes mature at an earlier age but not a larger size than slower-growing eels. The productivity of the habitat influences growth rate and, therefore, size and age at maturation. Thus, variation in length and age at maturity can occur in different habitats within a restricted geographic range. The length of the growing season and the temperature are negatively correlated with latitude, so age at maturity is strongly correlated with latitude. Both sexes display a time-minimizing strategy, i.e., they mature at the earliest opportunity. However, females mature at a larger size than males because they require sufficient energy to migrate to the spawning area and to produce eggs. Length at migration increases with distance to the spawning area for both sexes.

Metamorphosis Toward the end of the yellow phase, many morphological and physiological changes occur, transforming a bottom-oriented yellow eel into an oceanic, pelagic, migratory silver eel. Lipid in the muscle increases to 20–35% of

Table 2 Range of mean ages and mean lengths at maturity of silver eels of five species of *Anguilla*; the European eel is by far the most well studied in this regard

		Age at maturity			*Length at maturity*		
Species	*Sex*	*Mean age range (y)*	*Factor*[a]	*N*[b]	*Mean length range (cm)*	*Factor*	*N*
A. anguilla	Male	2.3–15.0	6.5	21	31.6–46.0	1.5	33
	Female	3.4–20.0	5.9	28	44.9–86.8	1.9	38
A. rostrata	Male	3.0–12.7	4.2	6	27.7–39.2	1.4	9
	Female	7.1–19.3	2.7	6	41.7–95.7	1.9	15
A. australis	Male	14.2–14.4	1.0	3	43.2–46.5	1.1	3
	Female	19.4–23.6	1.2	4	60.9–94.0	1.5	4
A. dieffenbachii	Male	23.2	—	1	62.3–66.6	1.1	2
	Female	34.3–49.4	1.4	2	106.3–115.6	1.1	2
A. japonica	Male	6.4	—	1	48.3	—	1
	Female	8.3	—	1	61.4	—	1

[a] Factor, largest value divided by smallest value.

[b] N, number of geographic locations studied.

muscle mass in European eels. The gut degenerates, suggesting that silver eels do not feed on migration. The eye increases in diameter by approximately 50%, the number of rod cells in the retina increases, and the spectral absorption maxima shifts more toward blue. This results in increased sensitivity for conditions in the oceanic mesopelagic zone by day and the epipelagic zone by night. The ventral surface of the body becomes whiter and more reflective, increasing the countershading. The swim bladder retial capillaries increase in length from yellow to silver eel, by a factor of 2.5 in American eels, increasing swim-bladder gas deposition rate. Additional guanine is deposited in the swim-bladder wall, reducing diffusive loss of gas. Premigratory silver American eels maintained swim-bladder inflation at a simulated depth of 150 m compared with 60 m for yellow eels.

Silver Eels

Silver eels return to the open ocean, migrate to the spawning area, spawn, and presumably die. The temperate species typically leave fresh and coastal waters in mid–late summer or autumn, earlier at higher latitudes than at lower latitudes. They are presumed to spawn at the next spawning season. However, the journey and spawning have not been witnessed for any species, so the biology of this oceanic stage is speculative.

The fecundity of eels increases exponentially with length, ranging from about 0.4 to 25 million eggs depending on species and size (**Table 3**).

Migrations in the Ocean

Silver Eels

In a telemetric study in an estuary, silver American eels migrated seaward by selective tidal stream transport. By ascending into the water column when the tide was ebbing and descending to the bottom when the tide was flooding, eels moved seaward in a saltatory fashion. Directed swimming may also be important in less strongly tidal estuaries.

In shallow waters of the North Sea, silver European eels have been shown by telemetry to maintain

Table 3 Fecundity (number of eggs) of females of four species of *Anguilla* over the size range of eels studied; estimates are probably least accurate for *A. anguilla*

	Smaller eels		*Larger eels*	
Species	*Length (cm)*	*Fecundity*	*Length (cm)*	*Fecundity*
A. anguilla	65	775 000	85	1 956 000
A. australis	50	410 000	95	3 901 000
A. dieffenbachii	70	1 009 000	145	21 374 187
A. rostrata[a]	45	1 447 000	115	23 357 000
A. rostrata[b]	50	646 000	75	2 949 000

[a] Estimate from Maine, USA, 45°N.

[b] Estimate from Chesapeake Bay, USA, 37°N.

travel in a given direction regardless of tidal direction, without direct contact with the sea bottom. They also have the ability to move along the tidal axis by selective tidal stream transport. How these mechanisms are used in actual migration is unknown. In deeper waters of the western Mediterranean Sea, silver eels also maintained approximately unidirectional movement for hours to days. They also made daily vertical migrations, moving upward at dusk to about 160 m and down at dawn to about 320 m.

Routes and rates of silver eel migrations in the open oceans are unknown. I infer from the morphological and physiological changes in the eye, the swim bladder, and the skin that occur at metamorphosis to the silver stage that migration occurs in the epipelagic and upper mesopelagic zones. A model of European eel migration, which combined oriented swimming toward the Sargasso Sea with modeled surface currents, predicted an arrival in the Sargasso Sea somewhat south (15–20°N) and east of where the smallest leptocephali have been captured. A second simulated arrival occurred later at about 28–30°N.

Four migrating females of the New Zealand longfin eel were tagged with archival 'pop-up' satellite transmitters, programmed to release after two or three months. All four moved eastward from the New Zealand coast as much as 1000 km. This technology may allow rapid advances in knowledge of silver eel migrations at sea, at least for females of the larger species.

Because the spawning areas of many of the species are ill defined, the lengths of migrations of many are unknown. Apparently, many of the tropical species spawn over deep water just off the edge of the continental shelves, e.g., the Celebes, Molucca, and Banda seas in the western Pacific. In contrast, the migrations of the temperate species are lengthy (**Table 4**) or presumed so.

Leptocephali

Leptocephali of American and European eels < 5 mm long are distributed between 50 and 300 m deep both day and night, perhaps indicative of the spawning depth of eels. Larger leptocephali perform daily vertical migrations, which increase in magnitude with increasing body size. Those 5–20 mm long descend from 50–100 m deep by night to 100–150 m deep by day. Those > 20 mm long are concentrated at 30–50 m by night and 125–250 m by day.

The classical account of the horizontal migration of leptocephali of American, European, and Japanese eels is gradual westward transport south of the subtropical convergences of the Atlantic and Pacific Oceans. The westward transport of the Japanese leptocephali is by the North Equatorial Current. The vertical migration of the leptocephali moves them into the Ekman layer at night, so wind drift influences the trajectories of leptocephali in addition to influence of deeper geostrophic currents. The leptocephali then become entrained in the strong western boundary currents, where

Table 4 Estimated lengths of migration of silver eels of three species of *Anguilla* from various locations to the approximate center of the spawning areas[a], assuming travel on a great circle route. Data arranged from south to north.

Species	*Location*	*Distance (km)*
A. anguilla	Tejo River, Portugal	4980
	Po River, Italy	8200
	Loire River, France	5600
	River Shannon, Ireland	4965
	IJsselmeer, The Netherlands	7025
	Lake Vidgan, Sweden	8300
	Thjórsá River, Iceland	5150
A. japonica	Pearl River, China	2840
	Shih-Ting River, Taiwan	2205
	Yangtze River, China	2605
	Hamana Lake, Japan	2135
	Naktong-gang River, South Korea	2480
A. rostrata	Mississippi River, Louisiana, USA	2265
	Cooper River, South Carolina, USA	1440
	Chesapeake Bay, Virginia, USA	1550
	Penobscot Bay, Maine, USA	2165
	St John's, Newfoundland, Canada	2840
	St Lawrence River, Quebec, Canada	3820

[a] Assumed spawning locations: *A. anguilla* 25°N 60°W; *A. japonica* 15°N 140°E; *A. rostrata* 25°N 68°W.

they are transported rapidly northward. The western species metamorphose and detrain from the Gulf Stream and Kuroshio, whereas the European leptocephali, not yet ready to metamorphose, continue eastward in the North Atlantic Current.

Some have recently claimed that European leptocephali swim toward Europe by a more direct route from the Sargasso Sea. Their arguments are spatial and temporal. First, leptocephali off the continent of Europe increase in mean length from south to north, suggesting a migration in that direction. However, European leptocephali are found in the Gulf Stream and the North Atlantic Current. There could also be other drift routes eastward, such as an eastward countercurrent associated with the subtropical convergence zone. Secondly, the length of larval life is claimed to be only about 6–7 months on the basis of presumed daily rings in otoliths, versus 2 years or more in the classical account. Whether the migration of European leptocephali is passive or at least partially active cannot currently be resolved. However, back calculation of birth dates on the basis of presumed daily rings of the leptocephali implies that spawning occurs throughout the year. Yet, small leptocephali of the European eel only occur in the Sargasso Sea during part of the year. Unless there is another spawning area and time, the oceanic data are incompatible with the otolith data.

Glass Eels

Somewhere, perhaps the edge of the continental shelf, metamorphosis from leptocephalus to glass eel occurs. My speculation is that the diurnal vertical migration of leptocephali brings them into contact with the sea bottom on the shelf, perhaps triggering both metamorphosis and a change in behavior.

In near-shore waters and in estuaries, glass eels use selective tidal stream transport to migrate against a net seaward flow. The circatidal vertical migration is probably phased to the local tidal cycle through olfactory cues. Whether the cross-shelf migration is drift on residual currents, selective tidal stream transport, or oriented horizontal swimming is unknown.

Genetics and Panmixia

How closely related the eel species are is controversial. Debate has focused primarily on the distinctness of the European and American eels, but applies to all *Anguilla*. European and American eels separate morphologically on number of vertebrae. The mean vertebral numbers are 114–115 and 107–108, respectively, with little overlap in ranges. J. Schmidt considered them separate during his extensive research in the North Atlantic in the early 1900s.

In 1959, D. Tucker offered the bold hypotheses that: (1) eels from Europe do not return to breed but die without spawning; (2) the two eels are not separate species but are ecophenotypes of the American eel, their distinguishing characters being environmentally determined during egg and early larval stages; and (3) European populations are maintained by offspring of American eels. A north–south temperature gradient in the Sargasso Sea was proposed as the environmental influence on number of myomeres and vertebrae. Tucker's hypotheses, though criticized immediately, called attention to the lack of knowledge of the breeding and oceanic biology of eels.

Today, Tucker's hypotheses fail on oceanographic and genetic grounds. The spawning areas of both species overlap considerably in space and time, and they stretch primarily zonally not meridionally. The northern limit of spawning of the two species seems to be the very feature that Tucker invoked to provide the environmental difference. The two are not subject to systematically differing temperature conditions. Small leptocephali captured in single plankton net tows in the spawning area segregate bimodally on myomere numbers.

Analyses of nucleotide sequences of mitochondrial DNA (mtDNA) and nuclear DNA from European and American eels show the two to be closely related but distinct species. There are small but consistent differences in cytological characteristics of at least 9 of the 19 pairs of chromosomes. Hybrids of the two species are found in low frequency in Iceland, indicating that genetic isolation is not complete.

From Schmidt came the idea that European and American eels were each panmictic, i.e., a single breeding population of each species. Examination of nucleotide sequences of both mitochondrial and nuclear DNA has been used to address the question, with mixed results. European eels with particular sequences collected over wide geographic areas from Morocco and Greece to Sweden and Ireland did or did not cluster geographically in different studies. One study suggested weak structuring of the population, with a southern group (North Africa), a western–northern European group, and an Icelandic group. Another suggested no geographic genetic differentiation.

The single study of the American eel using mtDNA showed no geographic structuring among samples collected from the Gulf of Mexico to the Gulf of

Maine, 4000 km of coastline. Japanese eels collected at seven sites in Taiwan, two in mainland China, and one in Japan, showed no geographic structuring. MtDNA analysis showed genetic similarity between *Anguilla australis* from Australia and New Zealand, suggesting they not be treated as subspecies.

Evolution and Paleoceanography

Two studies of evolutionary relationships among nine key species (seven in common) were based on sequence analysis of mtDNA. Both considered that the genus evolved originally in the eastern Indian Ocean, then the Tethys Sea, or Indonesian area, with one suggesting *A. celebesensis* and one suggesting *A. marmorata* as the ancestral species *A. japonica* and *A. obscura* branched off early. More recently evolved and in the same clade are *A. australis*, *A. mossambica*, *A. reinhardtii*, *A. anguilla*, and *A. rostrata*. *A. mossambica* and A. *reinhardtii* are sufficiently related that further molecular analysis may suggest a single species. The molecular phylogenies match well with groupings of V. Ege from 1939 based primarily on dentition. The exception is that Ege believed the Japanese eel was closely related to the Atlantic species, a relationship difficult to envision zoogeographically.

Anguilla is known from fossils in the early Eocene Epoch, perhaps 50 million years ago (50 Ma), and the family may date from 100 Ma. The evolutionary dispersal of the Austral-Asian species occurred during the time when Australia was moving closer to the Indo-Pacific islands and when the Indian subcontinent had broken from Africa and was drifting toward Asia. Invasion of the Atlantic by the ancestor of the two Atlantic species probably was through the Tethys Sea and its connection to the Atlantic between Africa and Asia. Closing of the Tethys Sea about 30 Ma isolated them. Separation of the closely related *A. australis* from the Atlantic ancestor must have occurred prior to the closing. The timing of the separation of *A. anguilla* and *A. rostrata* is problematic.

Fisheries and Aquaculture

Fisheries occur for glass eels, yellow eels, and silver eels in continental waters. All fisheries are for prereproductive stages. World catches of *Anguilla* reported to the Food and Agriculture Organization averaged 234 000 t (metric tonnes) in 1995–1998. Asia accounted for about 90% and Europe nearly 7%. Under-reporting of catches is probably widespread. These values are misleading in terms of impact because they combine fisheries for glass eels (a few thousand per kilogram) with fisheries for large silver female eels (a kilogram per eel).

Glass eel fisheries are heaviest on the Japanese eel and the European eel, with some commercial harvest of other species. At a peak in the 1970s, glass eel catch in the estuary of the River Loire, France, alone averaged more than 500 t annually. Glass eels are used for human consumption (e.g., in Spain and Portugal), for restocking rivers (e.g., in the Baltic Sea area), and primarily for aquaculture (e.g., in Asia and Europe).

Eel culture operations in Asia produce about 120 000 t annually, almost all in China, Taiwan, and Japan. In Europe, eel farms produced about 10 000 t of eels in 1998, mostly in Italy, The Netherlands, and Denmark. Wild and cultured eels are prepared as fresh fish, smoked fish, or kabayaki, traditional Japanese grilled eel with a soy sauce.

International trade in live eels and the development of large-scale eel culture has negative as well as positive consequences. European and American eels were accidentally or purposely introduced into Japanese rivers, where in some cases they dominate the eel fauna. In Taiwan, wells drilled to supply water to eel farms resulted in aquifer depletion and land subsidence. The nematode, *Anguillicola crassus*, which naturally coexists with the Japanese eel, was introduced into the populations of European and American eels. Larval and adult worms infest the swim bladder wall and lumen, with unknown effects on swimming ability of silver eels migrating at sea.

Status of Eel Populations

The status of the stocks is best known for Atlantic *Anguilla*. That of the European eel has been assessed frequently and that of the American eel recently by working groups of the International Council for the Exploration of the Sea. For yellow and silver European eels, fishery-dependent and fishery-independent trends have been largely downward in the last 20–50 years. For American eels, trends have been downward in the last 20 years from peaks in the late 1970s or early 1980s, to very low levels in many cases. It is unknown if those peaks represented unusually high population levels. However, loss of habitat and commercial fishing have contributed to declines.

Recruitment of young Atlantic *Anguilla* from the sea has declined. Long-term data on glass eel recruitment are available in The Netherlands, where the trend was dramatically downward in the 1980s to low levels through the 1990s. This is paralleled by the trend in commercial catch of glass eels in the estuary of the Loire River. The numbers of older yellow American eels moving upstream in the St Lawrence River at an eel ladder declined by three orders of magnitude from the early 1980s to 1999. Two to three order declines in upstream-migrating yellow European eels have occurred in Sweden over the last 50 years.

Whether or not recruitment declines are the result of lowered spawning stock is not known. It is possible that regime shifts in North Atlantic oceanic conditions have resulted in decreased survival of leptocephali at sea or in altered transport pathways for the leptocephali. There are negative correlations between the North Atlantic Oscillation Index, indicative of northern North Atlantic circulation patterns and productivity, and recruitment of glass European eels in The Netherlands (dating to 1938), and recruitment of yellow American eels in the St Lawrence River lagged by four years (dating to 1974).

See also

Current Systems in the Atlantic Ocean. Fish Larvae. Fish Migration, Horizontal. Fish Migration, Vertical. Florida Current, Gulf Stream and Labrador Current. Kuroshio and Oyashio Currents. Marine Fishery Resources, Global State of. North Atlantic Oscillation (NAO). Wind Driven Circulation.

Glossary

Abyssalpelagic Zone of the water column of the ocean encompassing depths between 2000 and 6000 m.

Anticyclonic Direction of atmospheric or oceanic circulation around an area of high pressure, clockwise in the Northern Hemisphere and anticlockwise in the Southern Hemisphere.

Benthic Organisms dwelling near, on, or in the bottom of the sea.

Catadromy Life cycle in which a species of fish breeds in the ocean, migrates into fresh water for growth, and returns to the sea at maturity.

Circatidal vertical migration Vertical movement by an organism in phase with the tidal cycle of 12.5 h, with vertical movement occurring during slack tides.

Clade A group of organisms, e.g., a group of species, sharing characteristics derived from a common ancestor.

Cline Geographic trend in some characteristic of a species or population.

Contranatant A migration against the direction of prevailing water current flow.

Countershading Color pattern of a pelagic species with a dark, sometimes mottled dorsal surface grading to a silvery ventral surface to reduce the contrast between the animal and its background.

Daily (diurnal) vertical migration Vertical movement by an organism in phase with the solar cycle of 24 h, with vertical movement occurring during dusk and dawn, usually upward at dusk and downward at dawn.

Denatant A migration along the direction of prevailing water current flow, usually involving drift of young stages.

Detritus Dead organic matter.

Ecophenotype The expressed characteristics of a particular subset of a genetically similar population caused by environmental conditions.

Ekman layer The near-surface layer, approximately 100 m deep, where wind-generated currents prevail.

Epipelagic Zone of the ocean encompassing approximately the upper 200 m.

Frontal zone Zone of the ocean in which the gradient (usually horizontal) in features of interest is steep, e.g., temperature, salinity, productivity, fauna.

Geostrophic current Currents in balance between a pressure-gradient force (gravity) and the Coriolis deflection.

Guanine A double-ringed nitrogenous compound forming part of a nucleotide found in DNA, but here also a crystalline substance deposited in the wall of a fish's swim bladder to reduce gaseous diffusion.

Ionic equilibrium Exhibiting equal concentrations of the same ions inside and outside an organism.

Isosmotic Exhibiting equal osmotic pressure inside an outside an organism.

Larvacean houses Delicate gelatinous cases secreted, and periodically discarded, by planktonic individuals of the Class Larvacea, Subphylum Urochordata, Phylum Chordata.

Leptocephalus The larval stage of eels of the Orders Anguilliformes and Saccopharyngiformes and of tarpons Order Elopiformes and bonefishes and spiny eels Order Albuliformes.

Meridional Distribution of oceanic characteristics or organisms on a north–south (longitudinal) axis.

Mesopelagic Zone of the water column of the ocean encompassing depths of 200–1000 m.

Mitochondrial DNA Genetic material of the mitochondria, the organelles that generate energy for animal cells, which is passed from female to offspring in eggs.

Molecular phylogeny Evolutionary relationships among taxonomic groups based on molecular techniques, especially the analysis of nucleotide sequences in DNA or amino acid sequences in proteins.

Myomere Muscle segment along the flank of a fish, here a larval eel.

North Atlantic Oscillation Index Difference in sea-level atmospheric pressure between Lisbon, Portugal (or Ponta Delgada, Azores) and Reykjavik, Iceland.

Nuclear DNA Genetic material of the nucleus of cells, a component of which is passed to offspring from both female and male parents.

Nucleotide Fundamental structural unit of the nucleic acid group of organic macromolecules, here those involved in information storage (in DNA: units containing adenine, cytosine, guanine or thymine), the sequences of which form codes for protein synthesis.

Otolith Concretions of calcium carbonate in a protein matrix deposited in the inner ears of bony fishes, frequently sectioned to examine annual or daily growth.

Panmixia The characteristic of a species being composed of a single breeding population.

Pelagic Areas of the ocean, or organisms dwelling, well away from the bottom of the sea.

Plankton Organisms in the water column of oceans and lakes that have weak swimming abilities, and are wafted by currents.

Recruitment The entry of organisms, typically fishes, into the next stage of a life cycle or into a fishery by virtue of growth or migration.

Regime shift A transition in oceanic conditions from one quasi-stable state to another.

Selective tidal stream transport Mechanism whereby an organism migrates along the tidal axis by ascending into the water column when the tide is flowing in the appropriate direction and descending to hold position near the bottom when the tide is flowing in the inappropriate direction.

Subtropical gyre Anticyclonic circular pattern of circulation in each of the major ocean basins between the equator and the temperate zone.

Subtropical convergence An area of the ocean where waters of differing characteristics come together, in this case equatorial and temperate waters meeting in the subtropical regions of the Northern and Southern Hemispheres.

Swim-bladder retia Countercurrent network of capillaries on the surface of a fish's swim bladder allowing gas pressure to increase and causing diffusion of gas into the swim bladder.

Western boundary current Western geostrophic currents of subtropical circulation gyres which are swift, deep, and narrow.

Zonal Distribution of oceanic characteristics or organisms on an east–west (latitudinal) axis.

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EKMAN TRANSPORT AND PUMPING

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Introduction

Winds blowing along the ocean's surface exert forces that set the oceans in motion, producing both currents and waves. Separating the wind force into the part that goes into making currents from that which goes into making waves is in fact very difficult. Conceptually, normal forces (i.e., think of the wind beating on the ocean surface like a drum) create waves, and tangential forces (i.e., frictional stresses exerted by the wind pulling on the sea surface) go into making currents. Although there are wind-generated currents that flow in a direction more or less downwind, the currents driven by the steady or slowly varying (compared to the period of the earth's rotation) wind stress flow in a direction