FISH MIGRATION, HORIZONTAL

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Introduction

Unlike migration in insects, for which migration usually entails emigration in response to unfavorable environmental conditions, fish migration usually involves an annual migration circuit, which each individual sustains for several years, sometimes decades. In temperate and arctic waters, where fish commonly occupy separate feeding and spawning areas at different seasons, migration usually involves an annual two-way journey, often over considerable distances.

Occurrence of Migration

There are about 800 species of freshwater fish. A further 12 000 species live in the sea and about 120 species move regularly between the two environments. There are only about 200–300 species in polar latitudes but many more in temperate waters. The majority (>75%) occur in the tropics, with as many as 500 species on a single reef. Most species are confined to fairly limited areas and their movements are generally limited to distances of less than 50 km. Several hundred species, however, include populations that migrate between widely separated areas. Migrations are often spectacular, covering distances of several hundred to several thousand kilometres; the annual circuits of some oceanic species (e.g., bluefin tuna) extend to 10 000 km. Migratory species sustain many of the world's large commercial fisheries. In 1998 (the most recent year for which FAO data are available) the total world catch of marine finfish was nearly 65 million tonnes from over 740 species. Forty percent of this catch was derived from 17 species (**Table 1**), all of which are considered to be migratory.

Terminology

Diadromous species migrate between the sea and fresh water. Anadromous species feed at sea but return to fresh water to spawn. Catadromous species, in contrast, spawn in the sea, after completing most of their postlarval feeding and growth in fresh water. Amphidromous species spawn in fresh water but feed in both environments. The larvae of amphidromous species emigrate soon after hatching and early feeding takes place in the sea; post-larvae or juveniles subsequently return to fresh water, where they feed, grow, and mature. The migrations

Table 1 Nominal world catches of the 17 most valuable species of marine finfish in 1998. Catches of these species comprised 40% of the total world catch of all marine finfish, which was 64.8×10^6 tonnes. Nominal world catches of diadromous species amounted to a further 1.8×10^6 tonnes

Species	*Catch (mt)*	*Catch (%)*	*Cumulative catch (%)*
Alaska (walleye) pollock, *Theragra chalcogramma*	4049317	15.62	15.62
Atlantic herring, *Clupea harengus*	2419117	9.33	24.95
Japanese anchovy, *Engraulis japonicus*	2093888	8.08	33.02
Chilean jack mackerel, *Trachurus murphyi*	2025758	7.81	40.83
Chub mackerel, *Scomber japonicus*	1910254	7.37	48.20
Skipjack tuna, *Katsuwonus pelamis*	1850487	7.14	55.34
Anchoveta (Peruvian anchovy), *Engraulis ringens*	1729064	6.67	62.01
Largehead hairtail, *Trichiurus lepturus*	1409704	5.44	67.44
Atlantic cod, *Gadus morhua*	1214470	4.68	72.13
Blue whiting, *Micromesistius poutassou*	1191184	4.59	76.72
Yellowfin tuna, *Thunnus albacares*	1152586	4.45	81.17
Capelin, *Mallotus villosus*	988033	3.81	84.98
European pilchard (sardine), *sardina pilchardus*	940727	3.63	88.61
South American pilchard, *Sardinops sagax*	937269	3.61	92.22
European sprat, *Sprattus sprattus*	696243	2.69	94.91
Round sardinella *Sardinella aurita*	663578	2.56	97.47
Atlantic mackerel *Scomber scombrus*	657278	2.53	100
Total catch of 17 most valuable species	**25928957**		

Data from Tables A-1(a) and A-1(e) of *FAO Yearbook*, Fishery Statistics, vol. 86/1, Rome, 2000).

of oceanodromous and potamodromous species are limited to the sea and fresh water, respectively.

Ecology

Life histories of migratory fish are geared to regional production cycles. Most bony fishes (teleosts) produce large numbers of pelagic eggs, which are carried passively by the prevailing current, until they hatch as yolk-sac larvae. The yolk sac provides an initial reserve of food, but the larvae must find a sufficient density of planktonic food if they are to survive once the yolk is exhausted. In tropical latitudes, where standing stocks are low and production is continuous, there is probably always enough food to ensure survival of moderate broods of larval fish and spawning can occur more or less continuously. In temperate and polar latitudes, however, production is discontinuous and, although standing stocks are much larger and capable of sustaining very large populations of fish, they are also much shorter-lived. In these regions, spawning is most successful when the larvae hatch at times of high food abundance. Eggs and early larvae are carried passively by the current, so reproduction is also most successful when spawning takes place upstream of a suitable nursery ground. Productive upwelling areas provide similar feeding opportunities for large stocks of fish in tropical and subtropical waters. The season is longer but production moves poleward during the summer, so here, too, reproductive success favors those species whose eggs hatch in the right place at the right time.

In many species spawning areas and spawning grounds are well defined and persist for many decades, possibly centuries. After recruiting to the adult stock, fish generally home to the same spawning ground, even though this may not be where they themselves were spawned. Most fish spawn annually through adult life, which may last several decades in unfished populations. In homing, many fish follow regular migration routes, which take them between their feeding and overwintering grounds and back to their spawning grounds. In some species (e.g., cod and herring), new recruits probably learn the migration route by accompanying the older fish on their way to the spawning grounds. Homing ensures that the adults return to a location from which it is probable that eggs and larvae will be carried to favourable nursery grounds at the start of each new generation. Spawning migrations compensate for the drift of eggs and larvae, and migratory fish stocks tend therefore to be contained within oceanic gyres. Fish that stray outside the gyre are generally lost to the parent stock.

Typical Life Histories

Anadromous Species

Anadromous species are found in a wide range of families that includes the Petromyzontidae (lampreys), Acipenseridae (sturgeons), Osmeridae (northern smelts), Retropinnidae (southern smelts), and Clupeidae (shads but not herrings). Salmon are by far the best known, with examples in both Atlantic (*Salmo*) and Pacific (*Oncoryhnchus*) genera.

Salmon typically lay their eggs in redds excavated in the gravel of a headwater stream. The alevins that hatch from the eggs remain in the gravel for some weeks before emerging as parr. Most Atlantic salmon (*S. salar*) parr spend up to 3 years in fresh water, before emigrating to sea as smolts, as do most Pacific species. In pink (*O. gorbuscha*) and chum (*O. keta*) salmon, however, the juveniles migrate to sea almost immediately after hatching. Most species spend several years feeding and growing at sea before they return to fresh water to spawn. Atlantic salmon spend 1–5 years at sea and fish from some European stocks range as far afield as West Greenland, where they mix with fish from the eastern seaboard of Canada and the United States; others go to the Norwegian Sea. Pacific salmon from North America migrate north to Alaska and then westward along the Aleutian Chain before moving out into the open ocean, where they mix with fish from Asia. Chinook salmon (*O. tshawytscha*) spend 5–6 years at sea, during which they probably make several circuits of the Gulf of Alaska before returning to US and Canadian rivers. Most adult salmon return to the river and stream in which they were themselves spawned. Once in coastal or estuarine waters, they find their way back by olfaction, following a specific home-stream odor, which appears to be produced by other fish of the same species. Most Pacific salmon die immediately after spawning; some Atlantic salmon return to the sea as kelts to spawn again after a further period of feeding in the sea.

Catadromous Species

Catadromy also occurs in a wide range of families that includes the Anguillidae (eels), Mugilidae (mullets), Galaxiidae (galaxiids and southern whitebaits), Cottidae (sculpins), Gobiidae (gobies) and Pleuronectidae (flounders). The life histories of anguillid eels, of which there are 15 species, are probably the best known.

Anguillid eels spawn at sea, usually in tropical to subtropical waters and often over great oceanic depths; they die after spawning. The eggs hatch as distinctive, leaf-shaped (leptocephalus) larvae, which have ferocious teeth and feed for one or more years as they are transported by ocean currents back to the continent from which their parents originated. The leptocephali metamorphose when they reach coastal waters and turn first into active, transparent, eel-shaped glass eels and then (up to a year later) into pigmented bottom-living elvers. Like salmon, elvers seek out fresh water by olfaction, although, unlike salmon, they appear to be attracted by the mix of odors produced by decaying detritus and associated microorganisms, rather than the odor of their conspecifics. Although there are substantial coastal eel populations, elvers enter fresh water in vast numbers. They move large distances upstream, disperse, grow, and become yellow eels, which spend up to 20 years in fresh water before reaching sexual maturity. A series of physical and physiological changes then turns the resident yellow eels into migratory silver eels, which move downstream to sea at night in the autumn, primarily during the first and third lunar quarters (the 'dark of the moon'). Feeding ceases, the gut atrophies, and silver eels rely on high fat reserves during their oceanic migration. Eye pigmentation also changes, so that peak spectral sensitivity shifts to the blue part of the spectrum, typical of clear oceanic waters. There are also changes in gas gland morphology, which allow the swimbladder to function in deep water during the oceanic spawning migration.

European (*Anguilla anguilla*) and American (*A. rostrata*) eels spawn in the Sargasso Sea within the Subtropical Convergence Zone, but in different locations. Spawning appears to be associated with areas of thermal density fronts. Some feature of southern Sargasso Sea water, possibly odor, may serve as a signal for returning silver eels to stop migrating and start spawning. Leptocephali of both species appear to be carried away from the spawning areas by gyres in the south-western Sargasso Sea, an Antilles Current, and the Florida Current north of the Bahamas. Thereafter they drift in the Gulf Stream and North Atlantic Current until they reach the American or European continental shelf. American eel leptocephali are found mostly in the west; European eel leptocephali are found all across the North Atlantic Current and its branches. The distribution of the larvae by size indicates that leptocephali take between 1.5 and 2.5 years to cross the North Atlantic. Despite some suggestions to the contrary, there are no reliable data to suggest that anything other than passive drift is involved. There may also be a more southerly migration route, originating in jetlike currents at the fronts in the western Sargasso Sea, which transport leptocephali toward the northern Canary Basin.

Amphidromous Species

The Japanese ayu (*Plecoglossus altivelis*), a small freshwater salmoniform, is a typical amphidromous species of the Northern Hemisphere. Demersal eggs are spawned in fresh water during autumn. On hatching, the larvae emigrate to sea, where they live for several months, before returning to fresh water during spring at a size of 50–60 mm. The fish grow and mature over the summer, before spawning and dying the following autumn. A similar life history is evident in a number of galaxiids in the Southern Hemisphere.

Oceanodromous Species

Life histories vary between oceanic and continental shelf species. The migration circuits of several species of tuna span whole ocean basins in both Northern and Southern hemispheres. The albacore tuna (*Thunnus alalunga*), for example, ranges over the entire North Pacific during its life (**Figure 1**); the southern bluefin tuna (*T. maccoyii*) occurs in both Pacific and Indian Oceans and may possibly make circumpolar migrations. Scombrids, which are closely related to tunas, are also migratory. The Western Stock of the Atlantic mackerel (*Scomber scombrus*), for example, which spawns over a large area of the Bay of Biscay along the edge of the continental slope, migrates to and from the Norwegian Sea,

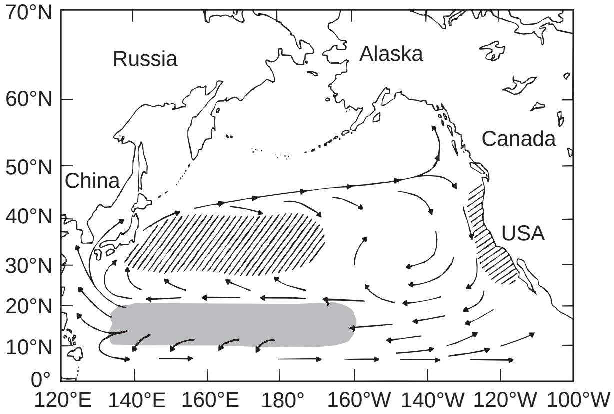

Figure 1 Distribution of albacore (*Thunnus alalunga*) in the North Pacific. The areas of the American fishery on young albacore and the Japanese fishery on older albacore are cross-hatched; the area in which the adults are believed to spawn is indicated by stippling. The main features of the subtropical gyre (Kuroshio, California, and North Equatorial Currents) and the North Equatorial Counter Current are shown by arrows. (From Harden Jones in Aidley (1980), with permission of Blackwell Science.)

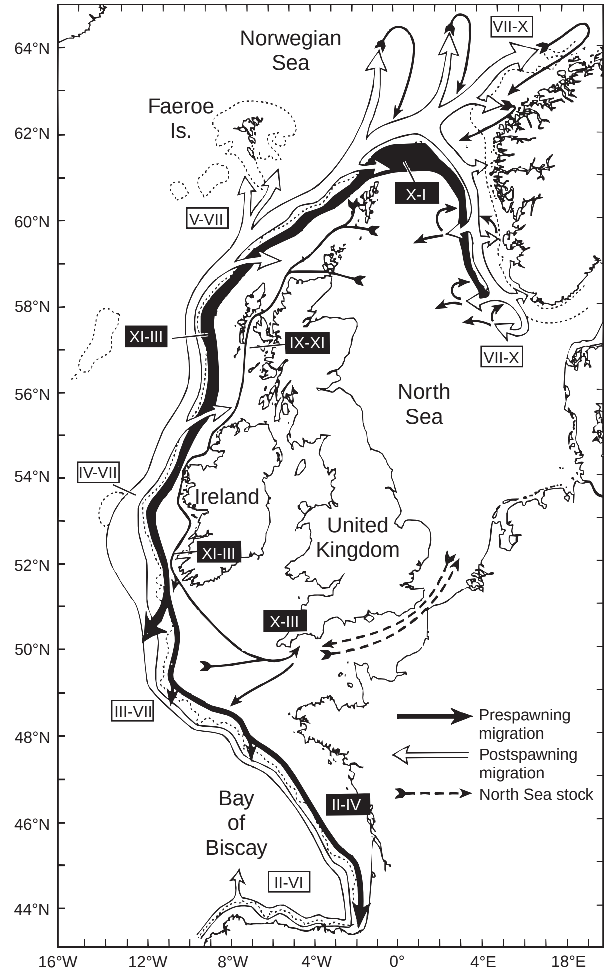

Figure 2 Inferred migration paths of the 'western stock' of Atlantic mackerel (*Scomber scombrus*). The Roman numerals indicate the months during which the fish are present in each area. (From SEFOS, Final Report to EU AIR Programme, May 1997.)

where it feeds in summer (**Figure 2**). Its migrations are possibly related to the northward-flowing European Ocean Margin Continental Slope Current. During the 1980s large, dense shoals of mackerel overwintered off the coast of Cornwall, where they formed the basis of a large fishery. Subsequently this behavior has changed and for unknown reasons the mackerel now overwinter much farther north.

The herring (*Clupea harengus*), another pelagic species, has many migratory populations. The Atlanto-Scandian herring, for example, which spawns off the southern coast of Norway in the spring, used to range through the Norwegian, Greenland, and Icelandic Seas, feeding at the productive polar front and wintering between Iceland and the Faeroes, along the boundary of the East Icelandic current. Following overfishing, the migration circuit changed and the stock now overwinters in Ofotfjord and Tysfjord, near Lofoten, where fish collect in immense, dense, and largely inactive shoals. The three stocks of North Sea herring – Buchan, Dogger and Downs – make similar, although much less extensive, migrations on the European continental shelf (**Figure 3**).

Many demersal species also have migratory populations. The Alaskan (walleye) pollack (*Theragra chalcogramma*), for example, the second most valuable species in the world (**Table 1**), occurs along the continental shelves of Asia and North America. In the Bering Sea, spawning occurs close to the Aleutian Islands in spring and summer, when dense shoals accumulate to the north of Unimak Pass (**Figure 4**). Spawning occurs between March and June, with a peak in May. Pelagic eggs, larvae, and young fish are distributed across the continental shelf by the local current system. At the end of the autumn the distribution contracts and with the

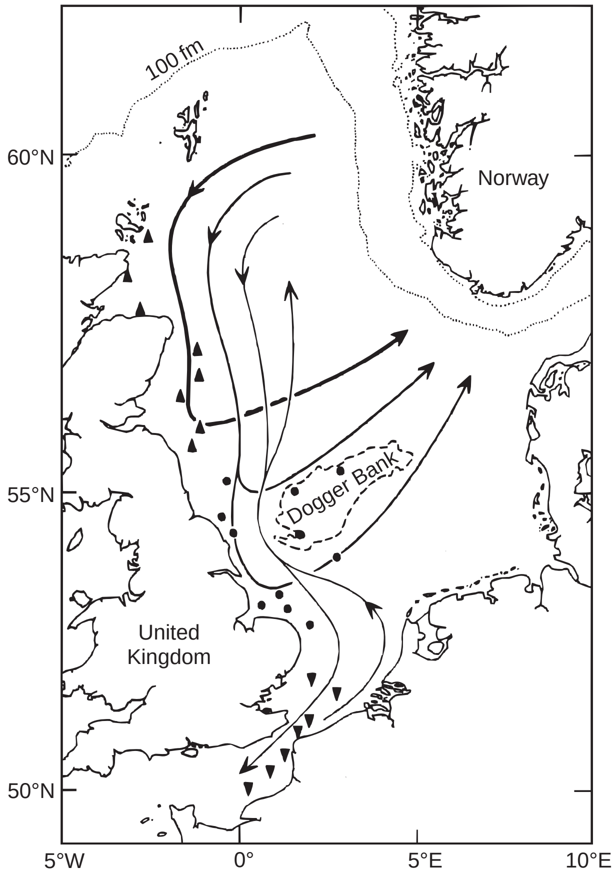

Figure 3 Migration routes and spawning grounds of three herring (*Clupea harengus*) stocks in the North Sea. (▲) northern North Sea (Buchan) summer spawners; (●) middle North Sea (Dogger) autumn spawners; (▼) Southern Bight and English Channel (Downs) winter spawners. The three groups share a common feeding ground in the northern North Sea. The Dogger Bank is shown by the dashed line. (From Harden Jones (1968, 1980), with permission.)

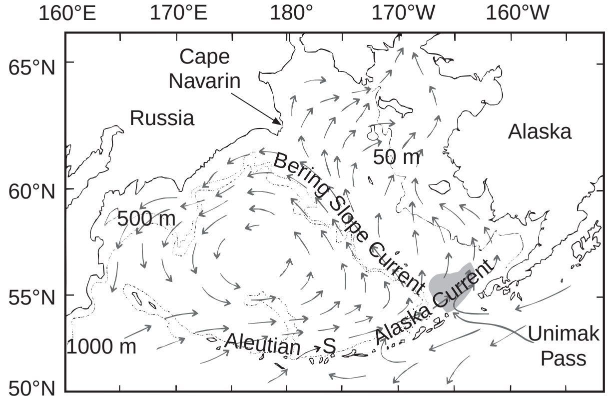

Figure 4 The spawning area (hatched) of Alaskan (walleye) pollack (*Theragra chalcogramma*) and the main surface currents in the Bering Sea. The migrations of older fish are related to the Bering Sea Slope Current and the distribution of larvae to the West Alaska Current. (From Harden Jones in Aidley (1981), with permission of Cambridge University Press.)

onset of winter the pollack return to the deeper waters on the edge of the shelf. The migrations of the adult fish appear to be related to the Bering Sea Slope Current (**Figure 4**), which flows north-west from the Aleutian Islands toward Cape Navarin in Russia.

The cod (*Gadus morhua*) has a comparable distribution in the North Atlantic, with separate stocks off the coasts of New England, Newfoundland, Labrador, West Greenland, East Greenland, Iceland, Faeroe. There are also stocks at Faeroe Bank and in the Irish Sea, North Sea, Baltic Sea, and Barents Sea. Greenland stocks are at the northern limit of their range and only produce large year-classes during the negative phase of the North Atlantic Oscillation (NAO) when eggs and larvae are carried to Greenland from spawning grounds off south-east Iceland. Juvenile cod can then reach Greenland in large numbers because of the increased flow of the Irminger Current produced by consistent easterly winds, a feature of the negative phase of the NAO at these latitudes. Large year-classes of cod at Greenland can result in dramatic increases in the fishery; in 1989, for example, catches at West Greenland exceeded 100 000 tonnes.

The Arcto-Norwegian cod stock feeds in summer over a large area of the Barents Sea between Spitsbergen and Novaya Zemlya (**Figure 5**). Large shoals collect in winter off northern Norway and at Bear Island, before migrating to coastal spawning grounds between the Murman coast of Russia and Romsdal in southern Norway. The West Fjord in the Lofoten Islands is the most important. After spawning, the spent fish return to the north, followed by the eggs and larvae (**Figure 6**), which are carried to the Barents Sea by the Norwegian Coastal Current (NCC). The depth at which the adult fish swim is unknown, but it is suggested that spent cod may occur near the surface, while maturing fish may possibly occur in the south-going countercurrent that underlies the NCC.

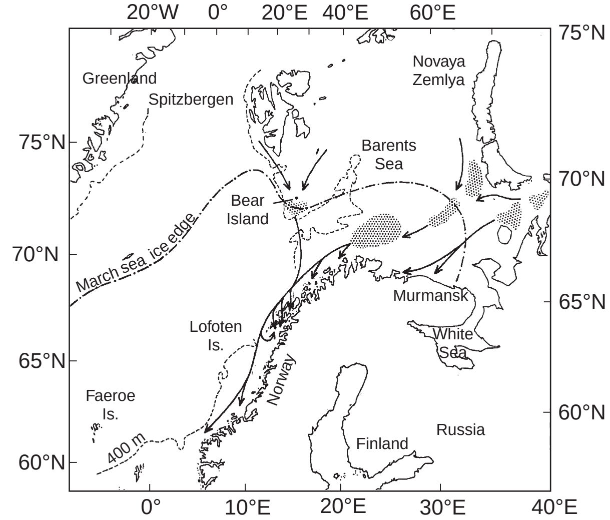

Figure 5 Autumn concentrations (stippled) and winter migrations of Arcto-Norwegian cod (*Gadus morhua*). (From Harden Jones (1968), with permission.)

The plaice (*Pleuronectes platessa*) is a typical flatfish, which is found throughout the shallow coastal waters of Northern Europe from the White Sea to the Mediterranean. In the North Sea there are four stocks, which spawn off the Scottish East Coast, Flamborough Head, and in the Southern and German Bights, respectively. Fish in the southern North

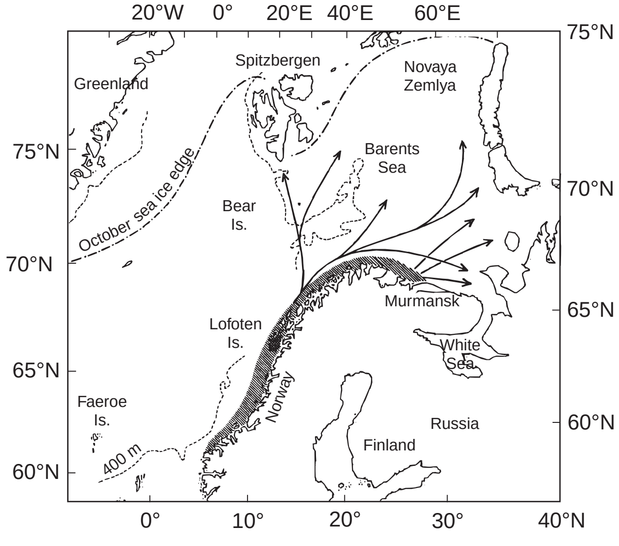

Figure 6 Spawning grounds (hatched) and postspawning migrations of Arcto-Norwegian cod (*Gadus morhua*). (From Harden Jones (1968), with permission.)

Sea are highly migratory and a proportion of the Southern Bight stock migrates through the Dover Strait to spawn in the eastern English Channel, where about 60% of spawning fish are of North Sea origin. Mature plaice move 200–300 km south in November and December to spawn in the Southern Bight and eastern English Channel. Peak spawning occurs in January and spent fish return north in January, February, and March. Meanwhile, the pelagic eggs and larvae drift north-east with the residual current flowing from the Atlantic through the Channel to the North Sea. The larvae take about 5–8 weeks to reach metamorphosis, when they become miniature flatfish. Most take to the bottom along the coasts of Belgium and Holland and many enter the Dutch Wadden Sea. Juvenile plaice leave their coastal nursery grounds and move to deeper water from their second year of life. Some larger males reach first maturity in their third year and join mature fish of earlier year-classes on the spawning ground during the latter part of the spawning season. Most first-time spawners migrate down the eastern side of the Southern Bight; most repeat spawners migrate up and down the English coast.

Mechanisms of Migration

Water is a fluid environment that is much more resistant to movement than air and contains very much less oxygen (3–5%) in the same volume. As a result, fish generally swim rather slowly, except when feeding or avoiding predators, when they can attain quite high speeds. Because cruising speeds are low – usually less than 1 fish length per second – water currents can have a significant effect on the ground track of the fish. They are a major factor for eggs and newly hatched larvae and are often important for adult fish too. Migrating fish may swim downstream in the direction of the current and it is then not clear whether the current provides directional information as well as transport, or whether the fish has an independent system of navigation. To resolve this fundamental question, it is necessary to measure the speed and direction of the water and the fish at the same depth, a virtually impossible task until the advent of electronic tags, modern sonars, and split-beam echo sounders.

The Role of Ocean Currents

There is a prima facie case that the migration circuits of many fish follow the oceanic gyres. Several species of Pacific salmon, for example, spend several years in the Alaskan Gyre and the route they follow on returning to the Fraser River is affected by the position of the Sitka Eddy, which governs whether they pass north or south of Vancouver Island. Southern bluefin tuna may follow the West Wind Drift around the Southern Ocean. Albacore tuna, which spawn between the Hawaiian Islands and the Philippines, appear to follow the clockwise movements of the Kuroshio, California, and North Equatorial Currents that make up the subtropical gyre in the North Pacific. The migrations of bluefin tuna, which spawn in the Gulf of Mexico and the Mediterranean, may also be linked to the subtropical gyre in the North Atlantic, although it is not yet known whether complete circuits of the basin are common. Two tagged bluefin, which in 1961 traveled a minimum distance of 4832 km from the Bahamas to Norway at an average speed of 40 km d^{-1}, almost certainly received substantial assistance from the Gulf Stream and its extension, the North Atlantic Drift. There are, however, as yet too few observations of the detailed movements of highly migratory fish to know whether they routinely follow the oceanic gyres, or only take advantage of the currents when it is energetically favorable.

The Role of Tidal Streams

Extensive fish tracking and midwater trawling studies in the North Sea have shown that several species of demersal fish – plaice, sole, flounder, cod, silver eels, and dogfish – make sophisticated use of the tidal streams (**Figure 7**) during their annual spawning migrations. Adult migrants show a 12-hour pattern of vertical movement related to the tides and juveniles of some species (e.g., plaice) show the same behavior. The fish leaves the seabed at one slackwater and spends about 6 h off the bottom, usually swimming in the upper half of the water column and often near the surface (**Figure 8**). It returns to the seabed around the time of the next slackwater and spends the ensuing tide on the bottom, not moving significantly (**Figure 9**). Flatfish bury in the sand during the adverse tide; roundfish probably refuge from the flow behind topographical features, where these are available. Fish using selective tidal stream transport progress rapidly in a consistent direction, determined by the choice of transporting tide. Prespawning and postspawning fish move in opposite directions and in the Dover Strait, for example; maturing and spent plaice can be caught in midwater on opposing tides in January.

Migration speed is determined by a number of factors, including the average speed of the tidal stream (commonly between 1 and 2 m s^{-1}), the size of the fish, and whether it uses all available tides. At various times, some fish use the transporting tide at

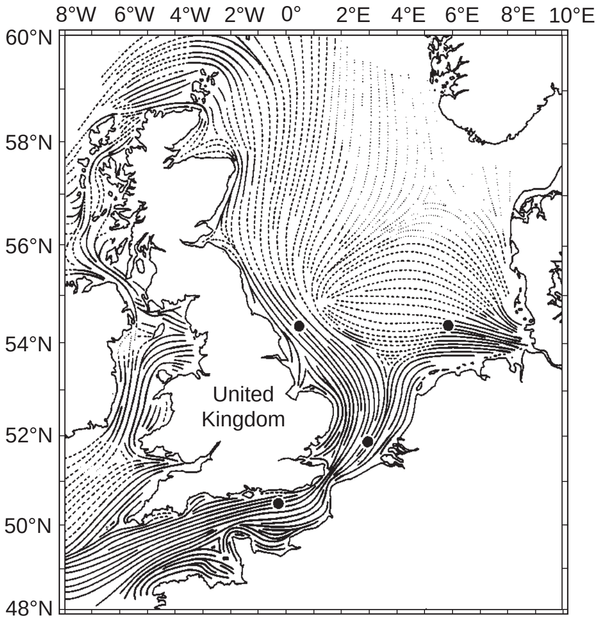

Figure 7 A tidal streampath chart for the North Sea and adjacent areas. The black circles indicate the centres of spawning of plaice off Flamborough and in the German Bight, Southern Bight, and eastern English Channel. (From Arnold in Aidley (1981) with permission of Cambridge University Press.)

night only; at other times, the same fish uses the transporting tide during the day as well. Fish using all transporting tides can move very rapidly (**Figure 10**) and visit more than one spawning area within a period of weeks. Vertical movements are usually well synchronized with times of local slackwater, although occasionally the fish remains in midwater over the turn of tide and is carried back some distance in the opposite direction. Recent studies have shown that migrating plaice save energy by heading downtide within ± 60° of the tidal stream axis and swimming through the water at a speed of approximately 0.6 fish length per second. For a 35 cm female plaice the saving on a typical annual migration circuit of 560 km is equivalent to 30% of the energy content of the eggs it spawns each year. Other recent studies indicate that plaice do not use tidal stream transport in areas of the North Sea where the speed of the tidal stream is insufficient for them to save energy. Instead they resort to other patterns of movement, which appear to be independent of the tidal streams.

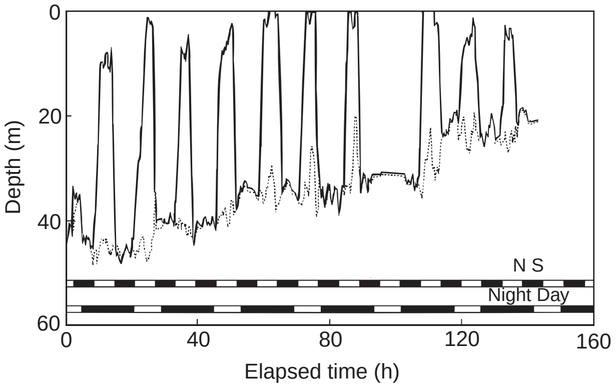

Figure 8 Vertical movements (solid line) of a 44 cm maturing female plaice tracked in the southern North Sea in January 1991. The dotted line indicates the depth of the seabed. The upper bar and lower bars indicate the direction of the tidal stream (north and south) and times of day and night, respectively.

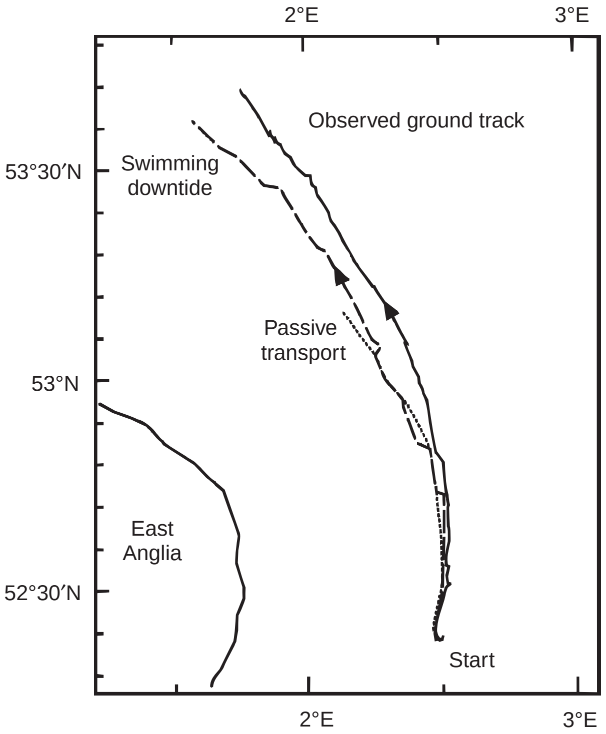

Figure 9 Geographical track of a 44 cm female plaice tracked in the southern North Sea in January 1991 (**Figure 8**). Also shown are computer simulations of how far the fish would have moved if it had been transported passively with the tide or had swum downtide at a speed of 1 fish length per second. The fish moved 152 km to the north in 6 days by selective tidal stream transport (British Crown Copyright).

Orientation and Navigation

There is ample evidence that fish can maintain a consistent heading over deep water in the open sea at night and thus obtain guidance from an external reference. The clue may well be geophysical in origin, possibly geomagnetic, although no fish has yet been shown to truly navigate, in the sense of knowing its geographical coordinates and adjusting its course to compensate for lateral displacement by a current. This ability has, however, recently been

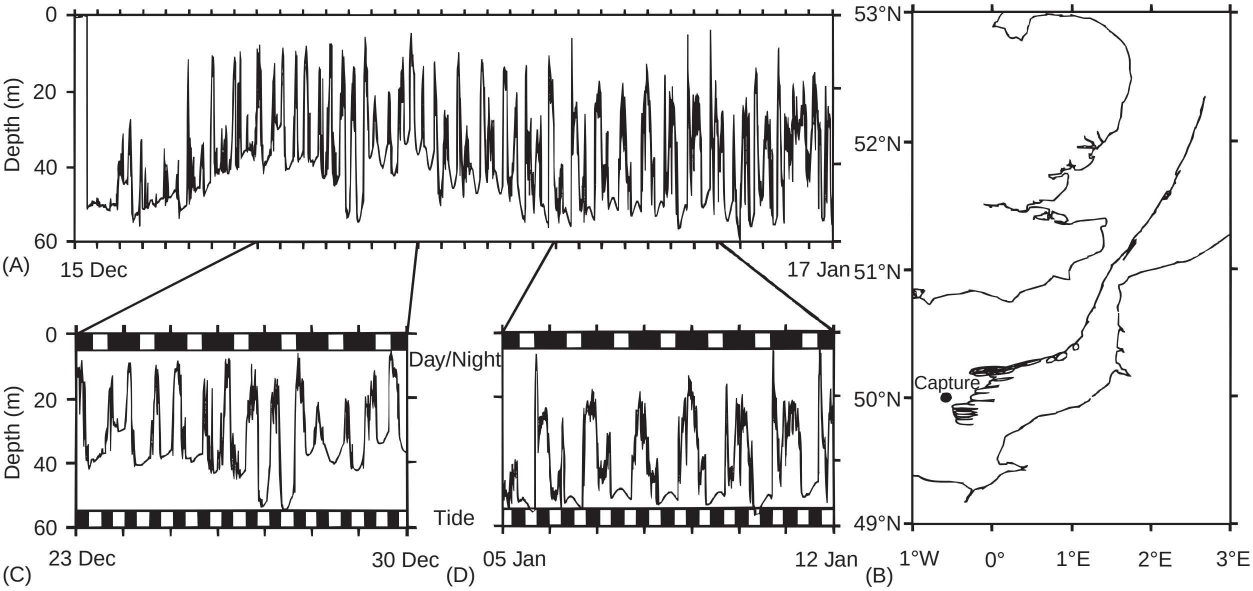

Figure 10 The reconstructed track of a 48 cm maturing female plaice fitted with a data storage tag, which recorded depth (pressure) at 10-minute and water temperature at 24-hour intervals. The track (B) was reconstructed from the vertical movements of the fish (A) and a computer simulation model of the tidal streams (**Figure 7**). During the first 7 days the fish showed selective tidal stream transport (C) and moved rapidly from the Southern Bight into the English Channel. During the remainder of the track the fish showed a diel pattern of vertical migration (D) and swam in midwater at night. It remained within the plaice spawning area in the eastern English Channel, where it was caught by a French trawler (British Crown Copyright).

demonstrated in green turtles (*Chelonia mydas*), during their postspawning migration from Ascension Island to Brazil. Individual turtles maintained remarkably similar courses for the first 1000 km, following the South Atlantic Equatorial Current in a west-south-westerly direction, possibly using chemical clues to remain in it. Subsequently, however, they began to compensate for southward displacement by the current and progressively corrected their course to head toward the easternmost part of the coast of Brazil. The data were obtained with radio tags, whose positions were determined by the Argos satellite system, which allows the movements of individual animals to be followed in detail over large distances with an indication of the accuracy of each estimated position. While ideal for marine animals like turtles, which spend most of the time at shallow depths and surface frequently, the Argos system cannot be used for fish, which, with the exception of a few unusual species, spend all their time submerged.

Discussion

Until the advent of electronic tags in the early 1970s, fisheries scientists had to rely on indirect information, such as catch rates and seasonal changes in distribution of fisheries, to deduce patterns of migration. Useful data could also be obtained from returns of conventional external tags, such as disks and streamers. Conventional tag data were, however, heavily biased by the distribution of fishing effort, which was often not well described. The returns could also not yield any information about the actual track of the fish between the release and recapture positions. In consequence, our knowledge about the mechanisms of fish migration and underlying sensory systems is based primarily on tracks of fish marked with acoustic tags and followed by research vessels. The technique has produced much useful information about migration on the continental shelves, but is not very suitable for the open ocean. It is also expensive, cannot be maintained for long periods, and does not readily permit the replication of observations. Increasingly, therefore, fisheries biologists are turning to archival (data storage) tags, which can record simple data such as depth, temperature, and light intensity for many months and retain them for several years. These data can be used to reconstruct the track of the fish in a variety of ways, depending on the behavior of the fish and the environment in which it lives. Archival tags can be deployed in large numbers and recovered through commercial or recreational fisheries. Alternatively, they can be programmed to detach from the fish after a pre-set interval and float to the surface, where they transmit data to a low-orbit satellite system, such as Argos. Although the data transmission capability of such systems is limited at present, the accelerating use of electronic tags is likely to lead to rapid advances in descriptions of the behavior of migrating fish and also an increased understanding of how they find their way around the oceans. Good descriptions of the migration circuits of the commercially exploited species should help to improve assessment, management, and conservation.

Conclusions

Fish spawn so that their eggs and larvae are carried to good feeding grounds for their juvenile stages. The adults must subsequently compensate for this drift, if the population is to sustain itself. As they grow, fish become less dependent on the environment and some may migrate without any reference to ocean currents at all. Adults of some species, however, still use the current if there is an energetic advantage in 'hitching a ride,' especially in shallow tidal seas. How fish find their way around the oceans and whether they can truly navigate, or only obtain guidance from local clues, is not yet known. There is, however, physiological evidence that fish do have a magnetic compass sense and behavioral evidence to suggest the involvement of geophysical, and perhaps also topographical clues. Rapid advances in understanding are to be expected in the near future with the increasing use of sophisticated electronic tags that allow the tracks of migrating fish to be described in detail over seasonal timescales and long distances.

See also

Antarctic Circumpolar Current. Current Systems in the Atlantic Ocean. Demersal Fishes. Eels. Fish Larvae. Fish Locomotion. Fish Migration, Vertical. Fish Predation and Mortality. Fish Reproduction. Fish Schooling. Florida Current, Gulf Stream and Labrador Current. Kuroshio and Oyashio Currents. Pelagic Fishes. Salmonids. Tides.

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FISH MIGRATION, VERTICAL

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Introduction

While the often spectacular long-distance migrations of fish have been well described by the scientific community and are the source of considerable wonder to the general public, fish can also undertake migrations in the vertical dimension. Such migrations can occur at the earliest life history stages when fish are free-swimming, and can continue throughout their lives. Some species exhibit vertical migration behavior at certain stages of their life history, but not in others. In general, vertical migrations occur with 24-h periodicity and, to a lesser degree, display constancy in phase and amplitude. Attempts to explain the regularity of changes in depth distributions of fish have often involved the notion of circadian or endogenous rhythmicity. The term 'circadian' refers to a self-sustained rhythm of 24-h periodicity, either synchronized to a natural cyclic phenomenon or free-running. When migrations (or other events) occur with 24-h periodicity,