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MESOPELAGIC FISHES

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Introduction

'Meso' meaning intermediate and mesopelagic (or midwater) fish refers to fish that live in the intermediate pelagic water masses between the euphotic zone at 100 m depth and the deep bathypelagic zone where no light is visible at 1000 m. Most mesopelagic species make extensive vertical migrations into the epipelagic zone at night, where they prey on plankton and each other, and thereafter migrate down several hundred meters to their daytime depths. Some species are distributed worldwide, and many are circumpolar, especially in the Southern Hemisphere.

Much research on distribution and natural history of mesopelagic fish was conducted in the 1970s, when FAO (Food and Agriculture Organization) searched for new unexplored commercial resources. The total biomass was at that time estimated to be around one billion tonnes with highest abundance in the Indian Ocean (about 300 million tonnes) approximately 10 times the biomass of the world's total fish catch. No large fisheries were, however, developed on mesopelagic fish resources, perhaps due to the combination of technology limitations and a high proportion of wax-esters, of limited nutritional value, in many species. From 1990 there was renewed interest in these species in connection with interdisciplinary ecosystem studies, when vertically and diel migrating sound-scattering layers (SSLs) turned out to be high densities of mesopelagic fish. These findings formed the basis for studies of the life history and adaptations of mesopelagic fish in the context of general ecological theory.

The thirty identified families of mesopelagic fish are listed in **Table 1** and typical morphologies are shown on **Figure 1**. The taxonomic arrangements of the families differ between various classification

Table 1 Families of mesopelagic fish with corresponding number of genera

Family	*Number of genera*	*Family*	*Number of genera*
Argentinidae	2	Alepisauridae	1
Bathylagidae	2	Scopelarchidae	5
Opisthoproctidae	4	Evermannellidae	3
Gonostomatidae	20	Giganturidae	2
Sternoptychidae	3	Nemichthyidae	ca.5
Stomiatidae	2	Trachypteridae	3
Chauliodontidae	1	Regalecidae	2
Astronesthidae	6	Lophotidae	2
Melanostomiatidae	ca.15	Melamphaeidae	2
Malacosteidae	4	Anoplogasteridae	2
Idiacanthidae	1	Chiasmodontidae	5
Myctophidae	ca.30	Gempylidae	20
Paralepididae	5	Trichiuridae	8
Omosudidae	1	Centrolophidae	1
Anotopteridae	1	Tetragonuridae	1

Adapted from Gjøsaeter and Kawaguchi (1980).

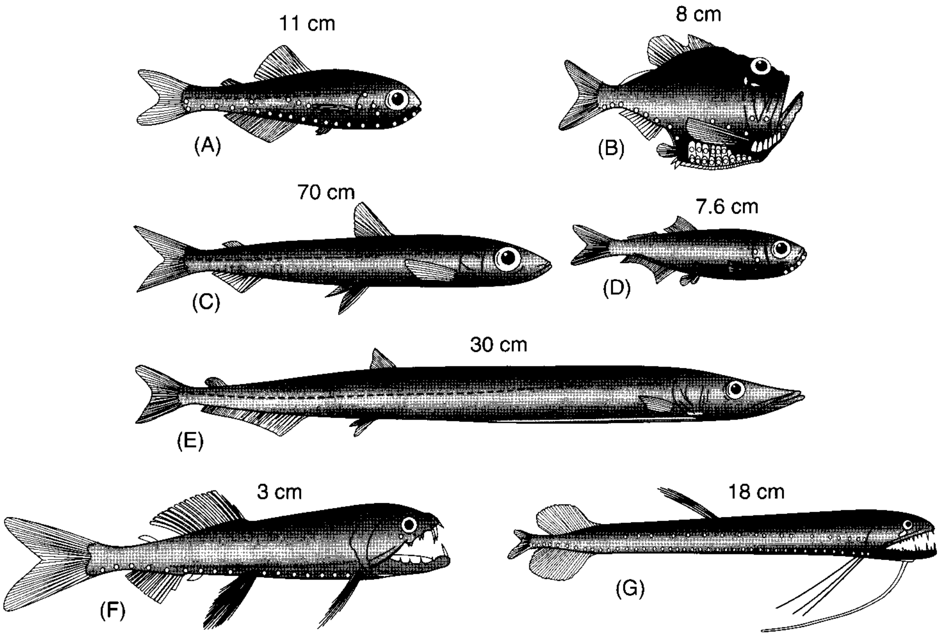

Figure 1 Mesopelagic fish. (A) *Benthosema glaciale* (Myctophidae. (B) *Argyropelecus olfersii* (Sternoptychidae). (C) *Argentina silus* (Argentinidae). (D) *Maurolicus muelleri* (Sternoptychidae). (E) *Notolepis rissoi kroyeri* (Paralepidae). (F) *Astronesthes cyclophotus* (Astronesthidae). (G) *Bathophilus vaillanti* (Melanostomiidae).

systems. In terms of the number of genera per family, the families Gonostomatidae, Melanostomiatidae, Myctophidae, and Gempylidae are the most diverse.

Mesopelagic fish are abundant along the continental shelf in the Atlantic, Pacific, and Indian Oceans and in deep fiords, but have lower abundance offshore and in Arctic and sub-Arctic waters. Most populations have their daytime depths somewhere between 200 and 1000 m. They show several adaptations to a life under low light intensity: sensitive eyes, dark backs, silvery sides, ventral light organs that emit light of a spectrum similar to ambient light, and reduced metabolic rates for deeper-living fish. Vertically migrating species have muscular bodies, well-ossified skeletons, scales, well-developed central nervous systems, well-developed gills, large hearts, large kidneys, and usually a swim bladder. The ventral light organs are species specific in some families, such as the Myctophidae. The deeper-living species have reduced skeletons, a higher water content in their muscles, lower oxygen consumption, and probably reduced swimming activity compared with species that live at shallower depths.

Life Histories

Most mesopelagic fish species are small, usually 2–15 cm long, and have short life spans covering one or a few years. Some species, especially at higher latitudes, become larger and older. A few larger species such as the blue whiting *Micromesistius poutassou* also live in the mesopelagic habitat, but have the characteristics of epipelagic species. Because of a generally small size, mesopelagic fish have low fecundity, ranging from hundreds to a few thousand eggs. This implies a low mortality in the early life stages, whereas adult mortality is high compared with many epipelagic species. Despite their low fecundity mesopelagic fish have a higher reproductive rate than long-lived epipelagic species which have higher fecundity but a much longer generation time. Neither eggs nor larvae from mesopelagic fish appear to have fundamentally different morphology from those of epipelagic fish, and the larvae all inhabit the epipelagic zone and have growth rates comparable with larvae of epipelagic fish. The higher survival among the early life stages of mesopelagic fish than of epipelagic species has not yet been quantified. One possible explanation could be different advective loss. The early life stages of large epipelagic populations are passively transported long-distances which means high advective loss. No particular long-distance drift pattern is yet known for mesopelagic fish and this may reflect lower advective loss and lower mortality.

Generally, mesopelagic species that live at high latitudes or at shallow depths have more defined spawning seasons than those that live deeper or at lower latitudes. Some species (e.g., *Maurolicus muelleri*, *Gonostoma ebelingi*, *Cyclothone pseudopallida*) exhibit batch spawning, with repeated spawning throughout a prolonged season of several months. Egg diameters do not differ from those of other fish with pelagic eggs and range between 0.5 and 1.65 mm. The eggs are released either in the daytime in deep water, or epipelagically at night. Eggs and larvae have a dilute internal milieu which makes them buoyant. In some species these buoyancy chambers are later replaced by a swim bladder. Other species, especially among the deepest-living forms, do not have a swim bladder. Those with a gas-filled swim bladder often deposit increased amounts of fat in the swim bladder as the fish become older. Before metamorphosis the larvae inhabit the productive epipelagic zone. During metamorphosis the skin becomes pigmented, light organs develop, and the young start to move down towards the adult habitat. Among some myctophids this ontogenetic shift in habitat is believed to be recorded in the otoliths as accessory primordia, that is, structures that appear as extra nuclei outside the true nucleus of the otoliths.

Growth and age composition of some species have been studied by counting presumed annuli or daily increments in the otoliths. In cold and temperate waters both annual and daily increments may be found. In tropical waters only daily increments can usually be detected, partly because of a shorter longevity in these waters and partly because of the lack of seasonality that fish from temperate regions experience. When there are seasonal changes in the environment this is usually registered as annuli in the otoliths. Only seldom has the periodicity of the increments been validated for mesopelagic fish, Nevertheless, studies have verified the daily basis of microincrements in, for example, *Maurolicus muelleri*, *Benthosema suborbitale*, *B. pterotum*, *B. fibulatum*, *Lepidophanes guentheri*, *Diaphus dumerilii*, *D. diademophilus*, *Lampanyctus* sp., and *Myctophum spinosum*. Annual increments have been partially validated for *M. muelleri*, *B. glaciale*, *Notoscopelus kroyeri*, and *Stenobrachius leucopsaurus*.

The usual pattern of growth towards an asymptotic size (usually expressed by fitting the von Bertalanffy growth equation to empirical data of length versus age), which is common in fish, may not occur in all mesopelagic species. Some show almost linear length increase with age and tend not to reach any asymptotic length in their lifetime. Others slow down their length increase as they become older but do reach an asymptotic length.

Among widely distributed mesopelagic species, geographical variation has been found in morphology, life history or genetics. Based on morphology, 15 subspecies of *M. muelleri* have been identified worldwide. Meristic characters of *B. glaciale* and *Notoscopelus elongatus* differ between the Mediterranean and the North Atlantic, which suggest genetic heterogeneity. Furthermore, populations of *B. glaciale* in west Norwegian fiords are genetically different from each other and from the Norwegian Sea population, and their life histories also vary, with a faster growth towards a lower maximum length in the fiord populations. Genetic isolation is probably possible because of the generally deep distribution of *B. glaciale* combined with relatively shallow sills at the mouth of the fiords. *Maurolicus muelleri* in Norwegian fiords have lower mortality than those in oceanic water masses. The estimated light level at the depth occupied by *M. muelleri* is also lower in the fiords than off the shelf, and this may give the fiord fish improved protection from visually oriented predators. The growth rate, reproductive strategy and predation risk also tend to differ between fiords.

Sexual size dimorphism is observed in many mesopelagic species as well as in numerous other fish species. In such dimorphic species the average size of females is larger than for males. Possible explanations for such differences are lower mortality and/or higher growth among females. In some species (e.g., *Cyclothone microdon*, *Gonostoma gracile*) sex change occurs; they change from male to female as they grow older. That females are larger than males indicates that a large body size is of greater benefit for females than males, possibly because large females are more fecund than small females. Secondary sexual characters are also found in some species. Among myctophids, males have a supracaudal light organ, whereas females have an infracaudal light organ. These light organs are perhaps structures that could be associated with courtship behavior.

Behavior

The behavior of mesopelagic fish has mostly been studied indirectly through monitoring of sound-scattering layers (SSLs) by echosounder and by pelagic trawling to obtain samples with some *in situ* sightings from submersibles. These show that mesopelagic fish are often oriented obliquely or vertically in the water column and it is thought that they may be in a dormant state during daytime. Fish with extensive vertical migrations are not good animals for laboratory experiments. Attempts to keep such light-sensitive mesopelagic fish in aquaria have failed because the fish attempted to migrate downwards, or battered themselves against the walls of the container until they became lifeless. In specially designed spherical containers with water jets, captured myctophid fish have survived a maximum of 72 h.

Although no long-distance horizontal spawning or feeding migrations are known for small mesopelagic fish, many species (particularly the myctophids and some stomiatoids) undertake nightly vertical feeding migrations into the productive surface layer. Species with gas-filled swim bladders are most prominent on the records of echosounders, and populations may appear as distinct layers. Such sound-scattering layers move upward after sunset and downward before dawn to their daytime depths. Vertical migration speeds up to $90\,\mathrm{m\,h^{-1}}$ have been measured. The entire population does not necessarily migrate to the surface every night. For instance, a considerable proportion of the adult population of *Benthosema glaciale* is present at daytime depths during the night, whereas juveniles are most numerous in the surface layers. Ontogenetic differences in daytime levels have been observed for *Maurolicus muelleri*. In winter and spring, juveniles are found in a separate scattering layer above the adults. Some evidence for depth segregation between the sexes is also reported; female *M. muelleri* tend to stay deeper than males at daytime during the spring in temperate regions. Depending on the season, females of *Lampanyctodes hectoris* have been reported to stay either shallower or deeper than males.

During daytime mesopelagic fish can adjust their vertical position to accommodate fluctuating light intensities caused by changes in cloudiness and precipitation. The adjustment of the daytime depth levels of the scattering layer thus suggests that vertically migrating mesopelagic fish tend to follow isolumes, at least over short time periods. However, during a 24 h cycle in the summer the estimated light intensity at the depth of *M. muelleri* has been observed to change by three orders of magnitude.

Light is a common stimulus for the vertical displacements and acts as a controlling, initiating and orientation cue during migration. It has been suggested that the ratio between mortality risk and feeding rate in fish, which locate their prey and predators by sight, tend to be at minimum at intermediate light levels. Thus, migration during dawn and dusk may extend the time available for visual feeding while minimizing the predation risk (so-called 'anti-predator-window'). At high latitudes in summer the nights become less dark, and the optimal vertical distribution for catching prey and avoiding predators is altered. For example, *Maurolicus muelleri* in the northern Norwegian Sea changes between winter to summer months from a daily vertical migration behavior to schooling. Schooling serves as an alternative antipredator behavior during feeding bouts in the upper illuminated productive water masses.

Adaptations

Mesopelagic fish experience vertical gradients in light intensity, temperature, pressure, rate of circulation, oxygen content, food availability and predation risk. Species of mesopelagic fish have adapted morphologically and physiologically to a midwater life in various ways. Mouth morphologies are generally large horizontal mouths with numerous small teeth, typical of fish that feed on large prey, combined with fine gill rakers, typical of fish that feed on small prey. This arrangement may partially explain their success, since it enables the fish to feed on whatever prey comes along, regardless of size.

Considered broadly, three main groups of mesopelagic fish can be identified based on the morphology: (1) small-jawed plankton eaters, mostly equipped with swim bladders; (2) large-jawed piscivorous predators with a swim bladder; (3) large-jawed piscivorous predators without a swim bladder. **Table 2** lists most of the traits that are typical for these groups.

The physiological and morphological adaptations in mesopelagic fish can be regarded as indirect or direct responses to light stimuli. For example, except for Omosudidae, all mesopelagic fish have pure-rod retinas which are characterized with a high density of the photosensitive pigment, rhodopsin. Eyes of mesopelagic fish tend to be large. The larger the absolute size of the eye and the greater the relative size of its pupils and lens, the better it is for gathering and registering the light from small bioluminescent flashes emitted by photophores. At times, such flashes may be frequent enough to merge into a nearly continuous background of light. Some mesopelagic fish (members of the families Gonostomatidea, Sternoptychidae, Argentinidae, Opistoproctidae, Scopelarchidae, Evermannellidae, Myctophidae, and Giganturidae) have even evolved tubular eyes with large lenses and a larger field of binocular vision, which improve resolution and the ability to judge distances of nearby objects. Coupled with short snouts such eyes enable the individuals to pick out small planktonic organisms in dim light. Tubular eye design for improved binocular vision is achieved at the cost of lateral vision. Many species have modified the eyes further with an accessory retina or even accessory lenses that also allow lateral vision.

Table 2 Organization of the major groups of mesopelagic fish. The comparisons of the predators are relative to the plankton consuming group

Features	*Mesopelagic planktivores*[a]	*Mesopelagic piscivores with swim-bladder*[b]	*Mesopelagic piscivores without swim-bladder*[c]
Colour	Often silvery sides	Black skin	Black and brassy
Photophores	Numerous and well developed in most species		
Jaws and teeth	Relatively short	Large jaws and teeth	
Eyes	Fairly large to very large, with large and sensitive pure-rod retina		Eyes and optic centers of the brain are moderately developed
Olfactory organs	Moderately developed in both sexes of most species		
Central nervous system	Well-developed in all parts		
Myotomes	Well-developed myotomes and large red muscle		Some reduction in myotomes, but still large red muscle system
Skeleton	Well ossified, including scales		Reduction in skeleton
Swim bladder	Usually present, highly developed		Regressed and invested by adipose tissue
Gill system	Gill filaments numerous, bearing very many lamellae to increase oxygen extraction at low ambient oxygen partial pressure		Not so well-developed
Kidneys	Relatively large with numerous tubules		
Heart	Large		
Metabolic rate	Decrease with increasing minimum depth		Low
Vertical position	Most of diel migratory fish belong to this group		Centered at lower rather than upper mesopelagic levels
Maturation age	Low	Higher	
Fecundity	Low	Higher	

[a] Families Gonostomatidae, Argentinidae, Sternoptychidae, Myctophidae and Melamphaeidae;
[b] Families Astronesthidae, Trichiuridae and Chiasmodontidae;
[c] Families Melanostomiatidae, Stomiatidae, Chauliodontidae, Malacosteidae, Scopelarchidae, Evermannellidae, Omosudidae, Alepisauridae, Anotopteridae and Paralepididae.
Families underlined have vertically migrating members.
Adapted from Marshall (1971) and Childress (1995).

The possibility of protection for mesopelagic fish lies in camouflage coloration which matches the light conditions in their habitat. Most of them lack spines or other protrusions that may serve as a defence against predators. In the deep ocean they find protection in twilight and darkness, where dark-skinned predatory fish are also well camouflaged. In shallower waters good camouflage is provided by transparency, by reflecting light to match the background perceived by a visual predator, or in certain surroundings by having a very low reflectance. The shallow-living larvae of mesopelagic fish are generally transparent to light. During and after metamorphosis, when the mature coloration is developing, the young fish move down to the dim or dark depths of their adult habitat. The adult coloration of a large proportion of the mesopelagic fish consists of silvery sides, a silvery iris, and a dark back. Most kinds of silvery-sided fish live at the upper mesopelagic levels, where, to the eyes of a visual predator, uncamouflaged prey will stand out against the background of light, except when viewed from above.

Silvery-sided fish are very vulnerable to attacks from below, particularly from black-skinned visual predators. When a visual predator looks upwards it will see its prey in silhouette. It has been argued that the ventral light organs in mesopelagic fish are an adaptation to emit light that matches the background of downwelling ambient light, in order to break up its silhouette and so to make attack from below more difficult.

The ability of mesopelagic fish, which are nearly neutrally buoyant, to undertake vertical migration is related to the structure of their myotomes. They have a muscular organization for sustained efforts with a large proportion of red muscle fibers. These are rich in fat, contain lots of glycogen, myoglobin, and many mitochondria and are richly supplied with blood and thus oxygen. White fibers that dominate the muscles of epipelagic fish, hold little or no fat, little glycogen, no myoglobin, few mitochondria and are more sparsely supplied with blood. White muscles work anaerobically in short bursts, such as rapid escape responses towards predators. The metabolic cost is related mostly to the requirements of the red muscle in moving the fish upward at a cruising speed in order to search for food. Little energy would be needed during descent when mesopelagic fish, whether they have a swim bladder or not, are likely to be negatively buoyant. The comparative development of red muscle in the tail of selected species is shown in **Figure 2**. Those with highest proportions of red muscle fibers undertake the most pronounced vertical migrations.

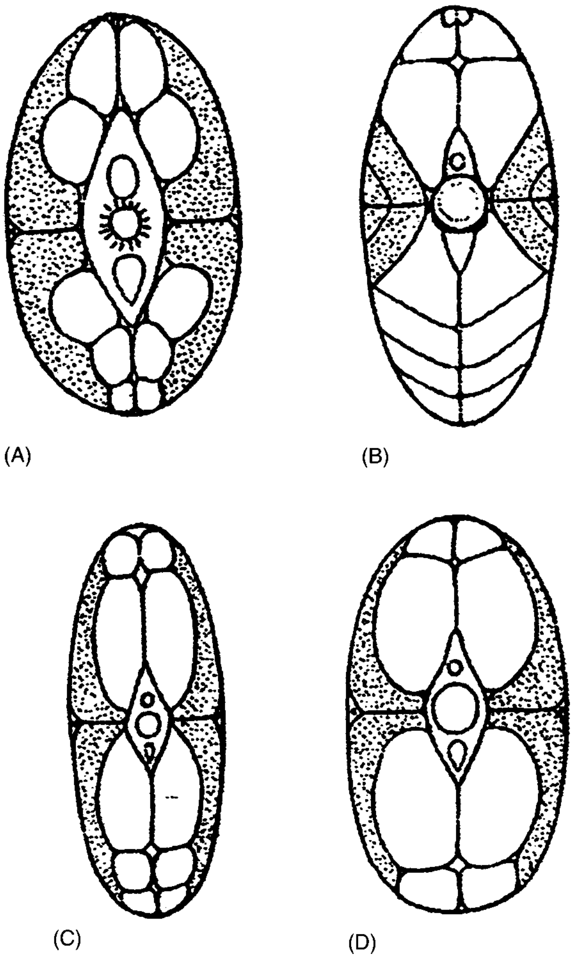

Figure 2 Transverse sections through the tails of three mesopelagic fish showing the extent of the red muscles (stippled). (A) *Notolepis coasti*, an Antarctic paralepidid. (B) *Electrona antarctica*, a myctophid. (C) *Maurolicus*, a Sternoptychidae. (D) *Astronesthes lucifer*. From Marshall (1977).

Originally the adaptive value of daily vertical migration was related to factors such as reduced competition among species through resource partitioning; minimizing horizontal displacement through advection; and bioenergetic benefits by foraging in warm surface waters and digesting in cooler deep waters. It was also suggested that mesopelagic fish could use vertical current gradients as a way of being transported to new feeding areas. Subsequently there has been more focus on the balance between predation risk and food demand and how this affects vertical distribution patterns. Emphasis has been laid on how vertical migration during dawn and dusk extends the time available for visual feeding, while minimizing the visibility towards predators. The earlier view relied on research in tropical and subtropical regions of the ocean where the fish always experience a change in temperature of about 10°C between the daytime depth and surface, and where also the daily light changes are similar all year round. Although similar temperature differences also exist during the summer in temperate regions, there is hardly any temperature difference between shallow and deep water in winter, and occasionally shallow water may be colder than the deeper water. The observations that mesopelagic fish also undertake daily vertical migration during the winter in west Norwegian fiords suggest that there are other explanations than bioenergetics. It is more likely that vertical migration extends the time available for visual feeding while minimizing the visibility towards predators. This is also consistent with the camouflage coloration in mesopelagic fish and that juveniles can stay in shallower water than adults because they are smaller, often transparent and thus less visible than adults.

There is a difference of a factor of 15 in metabolic rates between species that live at the surface and those that come no shallower than 800 m. This difference is found to be too great to be explained by decreases in temperature, oxygen content, decrease in food availability or increase in pressure. Comparative analyses of fish from different regions show similar depth trends even in isothermal regions (e.g., the Antarctic) for species which live at similar depths but at different oxygen concentrations. Several lines of research indicate that the metabolic decline is related to a reduction in locomotory abilities with increasing depth. It is suggested that the higher metabolic rates at shallower depths in groups with image-forming eyes is the result of selection action to favor the use of information on predators or prey at long distances when ambient light is sufficient. Hence, good locomotory abilities will be beneficial in order to escape predators. This idea is supported by the fact that major gelatinous groups that lack image-forming eyes do not show a decline in metabolic rate with depth. Thus, the lower metabolic rates found in fish living deeper where visibility is lower, result from the relaxation of selection for locomotory abilities, and is not a specific adaptation to environmental factors at great depths. If so, high metabolic rate in the surface waters indicates a metabolic cost of predation risk because good locomotory abilities require high metabolism. At greater depths the predation risk is much lower and the need for locomotory abilities decreases.

See also

Fiordic Ecosystems. Fish Feeding and Foraging. Fish Locomotion. Fish Migration, Vertical. Fish Predation and Mortality. Fish Reproduction. Fish Schooling. Fish Vision. Large Marine Ecosystems.

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MESOSCALE EDDIES

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Introduction

Mesoscale eddies are energetic, swirling, time-dependent circulations about 100 km in width, found almost everywhere in the ocean. Several modern observational techniques will be used to profile these 'cells' of current, and to describe briefly their impact on the physical, chemical, biological, and geophysical aspects of the ocean.

The ocean is turbulent. Viewed either with a microscope or from an orbiting satellite, the movements of sea water shift and meander, and eddying motions are almost everywhere. These unsteady currents give the ocean a rich 'texture' (**Figure 1**). If you stir a bathtub filled with ordinary water, it will quickly be populated with eddies: whirling, unstable circulations that are chaotically unpredictable. There is also a circulation of the water with larger scale, that is, broader and deeper movements. The 'mission' of the eddies is to fragment and mix the flow, and to transport quantities like heat and trace chemicals across it. In a remarkably short time (considering the smallness of viscous friction in water) the energy in the swirling basin will have greatly diminished. The bath will also cool much more quickly than one would estimate, based on simple conduction of heat across the fluid into the air above.