

Secrets of the Slime Hag

by Frederic H. Martini

*Loathsome though
they may seem, hagfishes
may also resemble
the earliest animals
to have a braincase—
making them even older
than the first animals
to develop a backbone*

DEAD WHALE on the deep-sea floor off the coast of California is aswarm with hagfishes. Scientists are finding that hagfishes—which have changed little over 330 million years of evolution—play important roles in the ecosystem of the ocean bottom, as both predators and scavengers.

Thump. After an hour of descending through near-total darkness in the research submarine *Alvin*, we slide into the silty ocean bottom roughly 1,700 meters (just over one mile) below the surface of the Pacific, off the coast of southern California. The pilot switches on the floodlights, illuminating a dense cloud of sediment kicked up by our arrival. Several minutes pass as we wait for the debris to settle and activate the sub's sonar system, which shows a large target roughly 240 meters away. As we move closer, we see through *Alvin*'s portholes the ghostly white carcass of a 32-metric-ton gray whale. The whale's watery grave is anything but peaceful: it is swarming with hundreds of half-meter-long hagfishes, which are methodically gnawing away at the whale's chalky blubber, bite by bite.

Scenes like this are eerie enough to keep some people up at night—and they change forever one's concept of burial at sea. But for my colleagues and me, who study the biology of hagfishes, they provide a fascinating glimpse into the lives of these strange and slimy animals. For years, the habits of hagfishes—which are sometimes called slime hags—and their place on the evolutionary tree of life have been a matter of conjecture. But recent studies indicate that hagfishes, which appear to have changed little over the past 330 million years, in many ways resemble the first craniates (animals with a braincase). For instance, the evolutionary path leading toward humans—and all other vertebrates (animals with a backbone)—probably diverged from that of hagfishes 530 million years ago. New research also shows that hag-



fishes are much more abundant—and probably play a much more important role in the ecology of the ocean-bottom community—than anyone would have guessed a decade ago.

Slime Balls of the Sea

The word “slimy” can only begin to describe the average hagfish: one good-size adult can secrete enough slime from its roughly 200 slime glands to turn a seven-liter bucket of water into a gelatinous mess within minutes. Hagfishes release slime in varying amounts, depending on the circumstances. They tend to produce slime in small amounts while feeding on a carcass, a behavior that might be designed to ward off other scavengers. But when attacked or seized, a hagfish can ooze gobs of goo, from all its slime glands at once. Although the slime is initially secreted as a small quantity of viscous, white fluid, it expands several hundred times as it absorbs seawater to form a slime ball that can coat the gills of predatory fish and either suffocate them or distress them enough to make them swim away. But for all its utility, the slime appears to be equally distressing to the hagfish. To rid its body of the sticky mucus, a hagfish literally ties its tail in a knot and sweeps the knot toward its head to scrape itself clean.

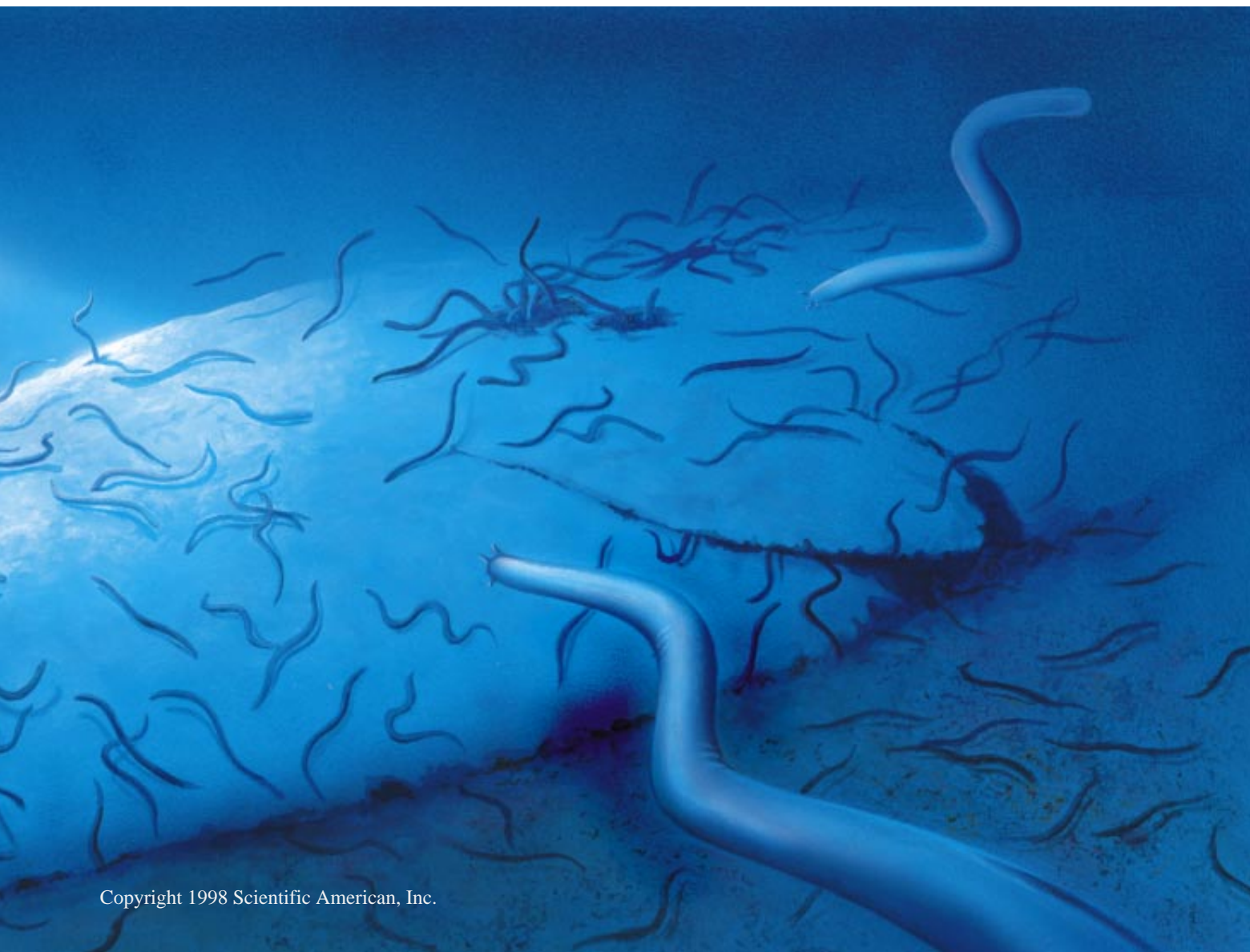
People often mistake the hagfish for an eel because both

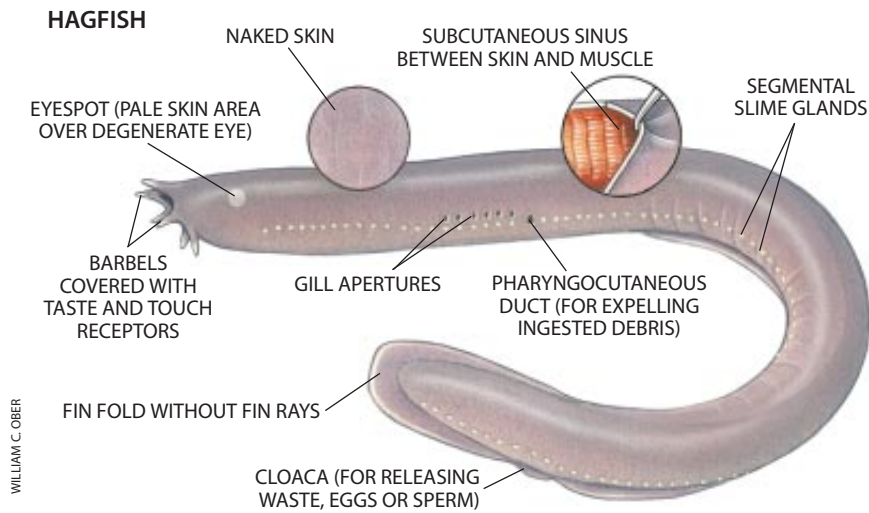
animals are long and cylindrical. The common names of several species of hagfish even include the term “eel,” usually accompanied by a descriptive adjective (“slime eel,” for example). As is so often the case, however, such common names are misleading. Hagfishes are not eels at all: true eels are bony fish with the requisite prominent eyes, paired pectoral and pelvic fins, a hard skeleton, bony scales and strong jaws. Like other bony fish, eels rely for respiration on gills that are attached to bones called gill arches and covered by a bony flap called an operculum.

In contrast, hagfishes are much simpler in form and function [see illustrations on pages 72 and 73]. They lack true eyes and paired fins, and their rudimentary skeleton consists only of a longitudinal stiffening rod made of cartilage, called the notochord, and several smaller cartilaginous elements, including a rudimentary braincase, or cranium. Hagfishes do not have scales; instead they have a thick, slippery skin and large, complex slime glands. In addition, they lack jaws, and their gills are a series of pouches that are different from the gills of any other living fish.

Hagfishes can be found in marine waters throughout the world, with the apparent exception of the Arctic and Antarctic seas. Although the animals always live near the ocean bottom, they can survive at a variety of depths. Water tempera-

ROB WOOD





EXTERNAL VIEWS of a Pacific hagfish (*left*) and an eel of the genus *Anguilla* (*right*) reveal that despite their similar shapes, the eel is a

the flesh, carrying it into the mouth. (The fang situated above the dental plates keeps live prey from wriggling away between bites.)

This feeding method works quite well when a hagfish preys on thin-skinned, soft-bodied sea worms, but the cusps cannot pierce the scales of fish or the skin of whales. Unless other scavengers have already opened the way, when feeding on a large carcass a hagfish usually takes the easy route, entering the body through the mouth, gills or anus. It then consumes the soft tissues from within, until only the bones and skin remain. More than one disappointed fisher has hauled in a prize fish that turned out to be a hollow shell full of hagfishes.

Only a few details are known about hagfish reproduction. Hagfish gonads form in a fold of tissue on the right side of the abdominal cavity. In a female an ovary forms in the anterior two thirds of the fold; in a male, a testis forms in the posterior one third. Curiously, individuals with both types of gonads are found occasionally. Females, which in some species outnumber males more than 100 to one, produce between 20 and 30 yolky, shelled eggs at a time. There are no oviducts; mature eggs are released into the abdominal cavity. The eggs—which vary in size from 20 to 70 millimeters, depending on the species—usually have hooked filaments at either end that enable them to lock together and be ejected in a chain. In males the testis produces sperm in follicles that release sperm into the abdominal cavity. Eggs or sperm then leave the abdominal cavity through a large pore into the

ture is the primary factor that limits the habitat of hagfishes: they appear to prefer waters cooler than 22 degrees Celsius (71 degrees Fahrenheit). In the cold coastal waters off South Africa, Chile and New Zealand, the animals sometimes enter the intertidal zone, where they have been collected in tide pools as shallow as five meters. In tropical seas, though, hagfishes are seldom seen at depths shallower than 600 meters.

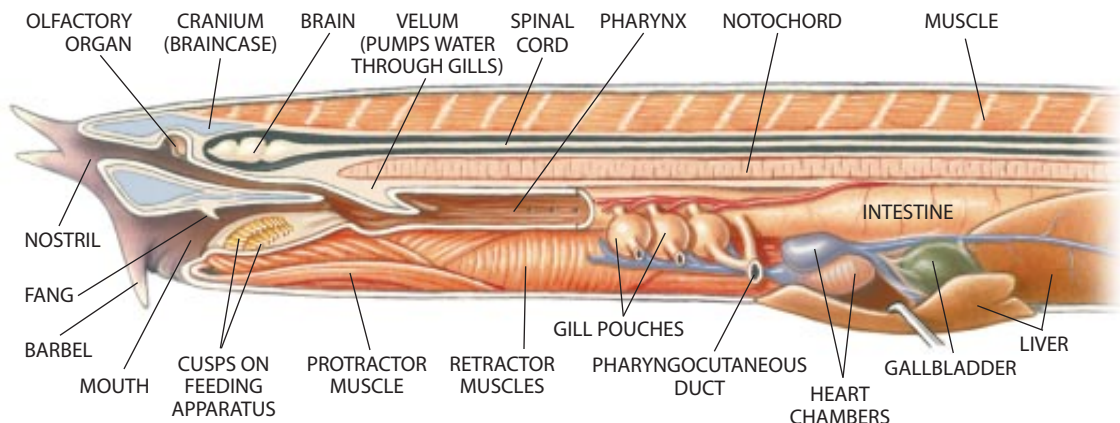
There are roughly 60 species of hagfishes, most of which are members of two major genera: *Eptatretus* or *Myxine*. (Many species in these genera, however, are known only from single specimens.) The genus *Eptatretus*, with roughly 37 species, includes the largest hagfish known, *E. carlhubbsi*, which can reach a length of 1.4 meters and can weigh several kilograms. Underneath their skin, *Eptatretus* species have the evolutionary remnants of eyes that are covered by translucent eyespots. Their heads also bear traces of lateral lines, sensory structures that extend down the sides of bony fish. Individual *Eptatretus* live in long-term burrows in the

ocean floor but may roam widely among rocks or other hard substrates.

Members of the genus *Myxine*, which includes roughly 18 species, are more specialized than *Eptatretus* for living in burrows. *Myxine* are generally more slender, have even more degenerate eyes that lack eyespots, and show no traces of lateral lines. Typical *Myxine* live in transitory burrows and are always found in or near soft, muddy sediments.

The feeding habits of hagfishes—which can eat small, live prey and act as scavengers—are particularly distinctive. As a hagfish feeds, it protrudes a very effective feeding apparatus consisting of two dental plates, each supporting two curved rows of sharp, horny cusps. The dental plates are hinged along the midline, allowing them to open and close like a book. To take a bite, a hagfish extends its feeding apparatus, causing the “book” to open, and presses the dental plates against a fleshy surface—whether it be the body of a sea worm, a dead fish or your hand. When the hagfish withdraws the apparatus, the book closes and the opposing cusps grasp and tear

ANATOMICAL VIEWS of the anterior (*left*) and posterior (*right*) parts of a Pacific hagfish highlight both the animal's unique specializations and other, more general characteristics—such as a cranium—that persist in more evolved animals. (The middle—roughly one third of the animal's length—has been omitted.) Like a small proportion of most species of hagfishes, this specimen has both an ovary and a testis.



more highly evolved, bony fish. Unlike the eel, the hagfish lacks jaws, paired fins, eyes, scales, dorsal fin rays, gill arches and gill covers.

cloaca, an excretory chamber that also receives and expels urinary and digestive wastes.

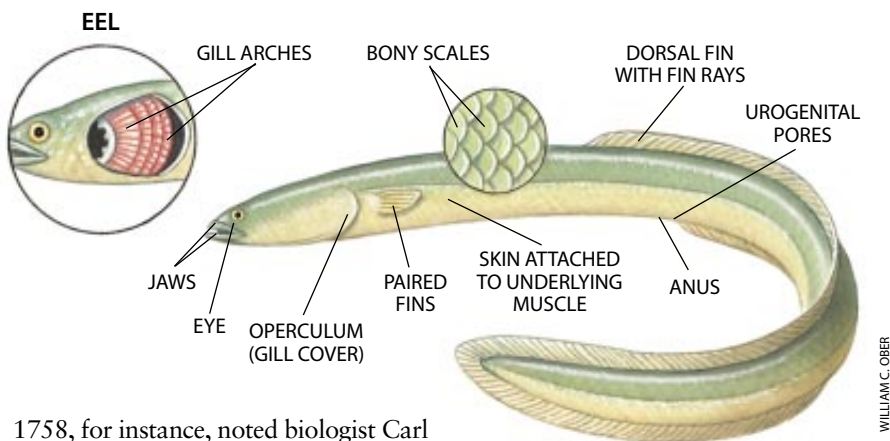
Apart from these anatomical details, however, the sex lives of hagfishes remain almost a complete mystery. We assume that hagfish females lay their eggs for subsequent fertilization by males, but we have no idea where, when or how this occurs. We also do not know why the sex ratio of the hagfish is biased toward females or how often the females produce eggs.

The embryonic development of the hagfish is also still a black box. Despite more than 100 years of searching, only three fertilized eggs of the genus *Myxine* have ever been found, and those were damaged. The situation is only slightly better for other genera of hagfish: roughly 200 fertilized eggs of the genus *Eptatretus* were collected in California's Monterey Bay between 1896 and 1942, but none have been recovered since.

Many other aspects of hagfish life are equally mysterious. For instance, juvenile *Myxine*—those under 170 millimeters in length—have never been collected. Where are they, and what do they eat? How fast do they grow? At what age do they mature sexually? As yet, we have no answers.

Living Fossils

Given the bizarre and mysterious biology of hagfishes, it is no wonder that these blind, jawless, scaleless, finless, bottom-dwelling creatures were not immediately recognized (or acknowledged) as distant cousins of humans. In



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1758, for instance, noted biologist Carl von Linné, writing under the name of Linnaeus, classified hagfishes as Vermes, or worms (rather than fishes), although we now know that hagfishes and worms are only distantly related.

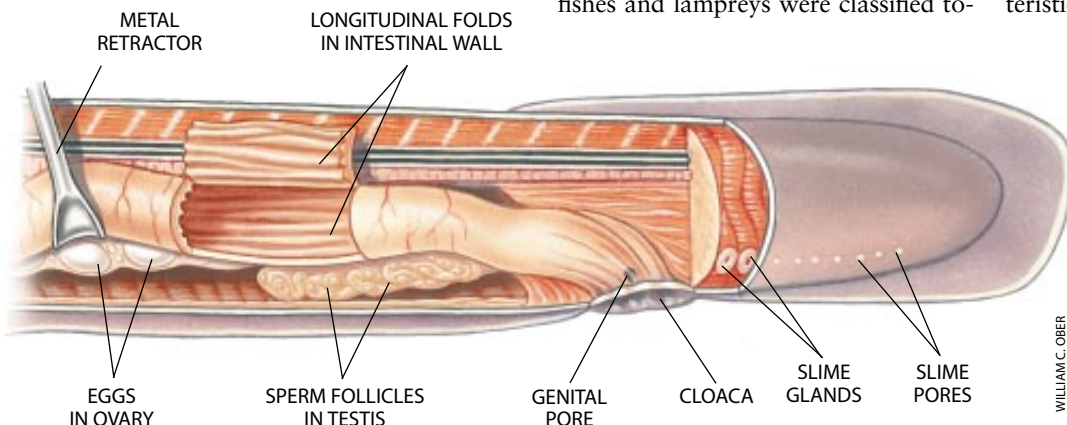
Today, however, scientists recognize that hagfishes are virtual biological time machines. The term "living fossil" is often used to refer to the coelacanth, a rare, deepwater fish with fleshy, lobed fins that was first caught in 1938 in waters off the east coast of South Africa, among the Comoro Islands. But hagfishes make coelacanths look like evolutionary newborns: coelacanths may have changed little since they first appeared in the fossil record 60 million years ago, but a fossilized hagfish, *Myxiniakela*, was found in sediments deposited roughly 330 million years ago. Aside from *Myxiniakela's* large eyes, if it were alive today it could easily pass for a modern hagfish.

Biologists neglected hagfishes for much of the past century primarily because of the way they classified animals. Until relatively recently, they relied on common features, such as the presence or absence of eyes or jaws, to establish relatedness between creatures. Under this scheme, hagfishes were lumped together with lampreys in a group called either Agnatha (literally, "no jaws") or Cyclostomata ("round mouths"). Hagfishes and lampreys were classified to-

gether because both lack jaws, paired fins, a bony skeleton and scales. Because the habitats of hagfishes make them relatively hard to come by, biologists concentrated on lampreys, which spend part of their lives in freshwater streams and rivers and therefore are much easier to catch.

In more recent years, the acceptance of phylogenetic systematics, or cladistics—classifying animals according to shared, specialized characteristics—has forced a reevaluation of the old methods for deciding what is related to what. Biologists now recognize that it is impossible to tell whether the ancestors of a given organism never had a particular feature or whether they had the feature but their descendants simply lost it sometime during evolution. Neither hagfishes nor snakes have legs, for example, but that does not mean that they are related. Hagfishes have never had paired fins—let alone limbs—but the ancestors of snakes had both forelimbs and hindlimbs.

According to cladistics, hagfishes and lampreys are separate and distinct groups within the chordates (Chordata) [see top illustration on pages 74 and 75]. At some point in their lives, all chordates display the following characteristics: a hollow, dorsal nerve cord; a notochord, situated immediately below the nerve cord; gill slits; and a segmentally muscled tail that extends past the anus. Hagfishes are considered the most primitive living craniates. Lampreys also have a cranium, but unlike hagfishes, they also have segments of cartilage to protect their nerve cord. These cartilage segments are the first evolutionary rudiments of a backbone, or vertebral column. Lampreys, there-



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fore, are considered the most primitive living vertebrates.

By comparing fossils with living creatures, biologists can create diagrams called cladograms that display the evolutionary relations among organisms. A cladogram of the chordates suggests that the hagfish diverged from the vertebrate evolutionary line around 530 million years ago. It also reveals that the predecessors of the hagfish never had a bony skeleton but that those of the lamprey did. What is more, the cladogram suggests that all early craniates had a complex protrusible feeding apparatus comparable to that of hagfishes. Early vertebrates, including the distant ancestors of humans, probably shared many other anatomical and physiological characteristics with modern hagfishes. But hagfishes have evolved many unique specializations: their eyes and lateral lines regressed, and they developed slime glands.

Besides their key position on the tree of life, hagfishes are also gaining new respect as members of the complex ecosystem of the ocean bottom. Scientists now know that the animals are more abundant than was once thought. Based on trapping surveys done between 1987 and 1992, my colleagues and I estimated that the inner Gulf of Maine contains population densities of up to 500,000 *M. glutinosa* per square kilometer. W. Waldo Wakefield of Rutgers University, who was then at the Scripps Institution of Oceanography, found comparable densities of *E. deani* off the California

EVOLUTIONARY TREE, or cladogram, shows that hagfishes are the oldest surviving craniates (animals with a braincase)—predating lampreys, cartilaginous fishes and ray-finned fishes by millions of years. (Fossils are indicated in italics.)

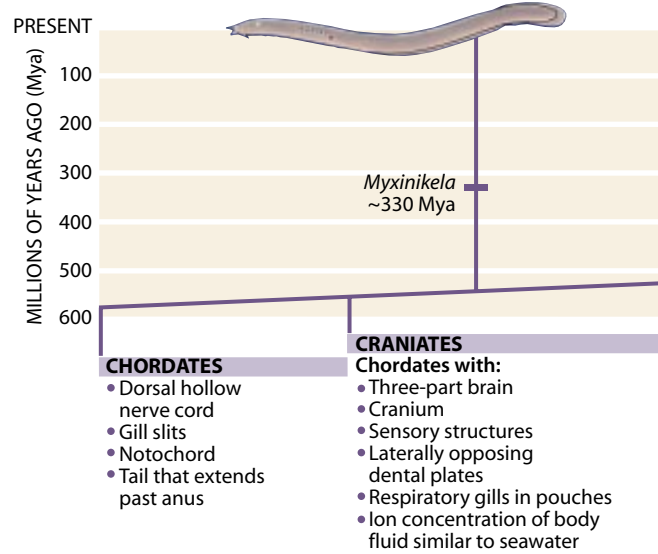
coast at depths of between 600 and 800 meters.

We also now recognize the degree of hagfish predation on the populations of other animals that live near the bottom of the ocean. Although individual hagfishes have extremely low metabolic rates, their energy needs add up. The average number of *M. glutinosa* that inhabit one square kilometer of seafloor (59,700 animals) must consume the caloric equivalent of 18.25 metric tons of shrimp, 11.7 metric tons of sea worms or 9.9 metric tons of fish every year. And that amount would be sufficient only to keep the animals alive at rest; when they swim or burrow, their energy demands increase between four and five times.

Hagfishes also consume discarded so-called bycatch from commercial trawling fleets and play a central role in recycling the carcasses of dead marine vertebrates, including whales. Craig Smith of the University of Hawaii has found that hagfishes can remove roughly 90 percent of the energy content of

HAGFISHES

Specializations:
Degenerate eyes; reduced lateral lines; barbels; slime glands; unique chemical receptors; pharyngocutaneous duct



small packages of bait sunk to the seafloor at depths of 1,200 meters. But hagfishes are not just important ecologically for their roles as predators or scavengers, they also serve as important prey for a surprising number of marine animals, including codfish, dogfish sharks, octopuses, cormorants, harbor porpoises, harbor seals, elephant seals and some species of dolphins.

The Slime Hag Trade

In many locales around the world, hagfishes have become the focus of a large and flourishing commercial fishery. Since the 1960s there has been a booming trade in leather goods produced from tanned hagfish skin. These products, which are manufactured primarily in South Korea, are sold as “eel-skin” (presumably because consumers would be less likely to pay high prices

PACIFIC HAGFISHES are on display at the Steinhart Aquarium in San Francisco (*top and bottom left*); the dissected dental plate of a preserved hagfish (*bottom center*) reveals its toothlike cusps. A photograph from a fishing boat (*bottom right*) shows a characteristic ball of slime.



LAMPREYS

Specializations:

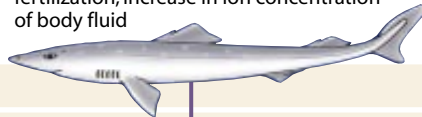
Larval stages and complex metamorphosis; oral sucking disk; parasitic habits (in adults); loss of bone



CARTILAGINOUS FISHES

Specializations:

Characteristic scales; claspers on males for internal fertilization; increase in ion concentration of body fluid



First "modern" sharks
~150 Mya
Hybodus
~240 Mya

Cladoseleche
~400 Mya

RAY-FINNED FISHES

Specializations:

Characteristic scales; dorsal fin rays articulating with individual skeletal elements within body



First "modern" ray-fins (teleosts)
~150 Mya

Andreolepis and *Lophosteus*
~410 Mya

Mayomyzon
and *Hardistiella*
~340 Mya
Jamoytius
~450 Mya

VERTEBRATES

Craniates with:

- Segmental cartilages protecting spinal cord
- Two semicircular canals in inner ears
- Ion concentration of body fluid roughly one third that of seawater
- Bone formation in skin layer

GNATHOSTOMES

Vertebrates with:

- Jaws
- Paired fins
- Three semicircular canals in inner ears
- Respiratory gills on gill arches
- Ducts to expel sperm or eggs

OSTEICHTHYES

Gnathostomes with:

- Internal bony skeleton
- Lung or swimbladder connected to gut
- Unique muscle pattern of jaw and gill regions

Lobe-finned fishes and tetrapods (amphibians, reptiles, birds, mammals)

JANA BRENNING AND WILLIAM C. OBER (drawings)

for goods labeled "slime-hag hide").

Hagfish skin, which is smooth and slick to the touch, consists of a superficial layer of epidermis overlying a dermis containing multiple, dense layers of collagen fibers. In the leather preparation process, the epidermis is removed, and the treated dermis is used to produce designer handbags, shoes, wallets, purses, briefcases and so forth. Removing the skin is relatively easy because it is attached to underlying muscles only along the dorsal midline and along the ventral surface at the level of the slime glands. Thus, the leather produced by one hagfish is a long strip, with a wrinkled band down the midline marking the site of the dorsal attachment to muscle.

The demand for suitable skins has supported commercial hagfish ventures around the Pacific Rim and in the western North Atlantic. The strip of skin must be above a minimum width (roughly five centimeters) but must not be too thick. This combination eliminates many species from the fishery: some are too small or too slender, others too large and too thick-skinned. The collection method is very low tech: multiple traps baited with anything from herring to kitchen scraps are set along a line on the

sea bottom and left overnight. The traps can be 19-liter pails with lids or 190-liter barrels with small holes in the sides; once inside, most hagfishes become trapped in the bait and their own slime. In previously unfished areas, more than 100 hagfishes have been found to enter a given trap during its first hour on the bottom.

Unfortunately, the demand for hagfish skin has depleted the populations of many species because the trapping rate has far exceeded their rate of reproduction. And as each species becomes less abundant, fishers target others. Over the past three decades, fishers have exploited *Paramyxine atami*, *E. burgeri*, *E. okinoseanus* and *M. garmani* in the western North Pacific, *E. stouti* and *E. deani* off the Pacific coast of North America, and *M. glutinosa* in the Gulf of Maine.

In the region of New England, annual landings of hagfishes went from virtually zero in 1991 to roughly 1,950 metric tons in 1996. Over that five-year span, roughly 50 million hagfishes were processed and shipped overseas. Fishers discard hagfishes that are shorter than 500 millimeters—the minimum length suitable for leather—and these usually

die when released into the comparatively warm surface waters. Accordingly, the actual impact of fishing on hagfish populations is far greater than indicated by the landings alone. By 1996 there were signs that hagfish fisheries were in trouble; recent declines in landings, average size and catch per trap suggest that the trouble is serious.

This state of affairs is not likely to improve, because almost everywhere hagfishes are classified as "underutilized species," and their exploitation is usually permitted without efforts to regulate the effect on hagfish populations. Hagfish trapping was considered a growth industry in New England, for example, when other fisheries were nearing a state of collapse.

Although hagfishes are more plentiful than once thought, we do not yet know enough about them to manage a sustainable hagfish fishery. In the meantime, we should take simple steps—such as requiring holes in commercial traps through which small, young hagfishes could escape—to reduce the impact on hagfish populations. When we drastically reduce the number of any species—even the lowly (and to some, loathsome) hagfish—we are performing an ecosystem experiment on a grand scale. As usual, we cannot yet begin to predict the eventual results. 5A

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Further Reading

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- THE HAGFISHERY OF JAPAN. Aubrey Gorbman et al. in *Fisheries*, Vol. 15, No. 4, pages 12–18; July 1990.
- THE BIOLOGY OF HAGFISHES. Edited by J. M. Jørgensen, J. P. Lomholt, R. E. Weber and H. Malte. Chapman & Hall, 1998.