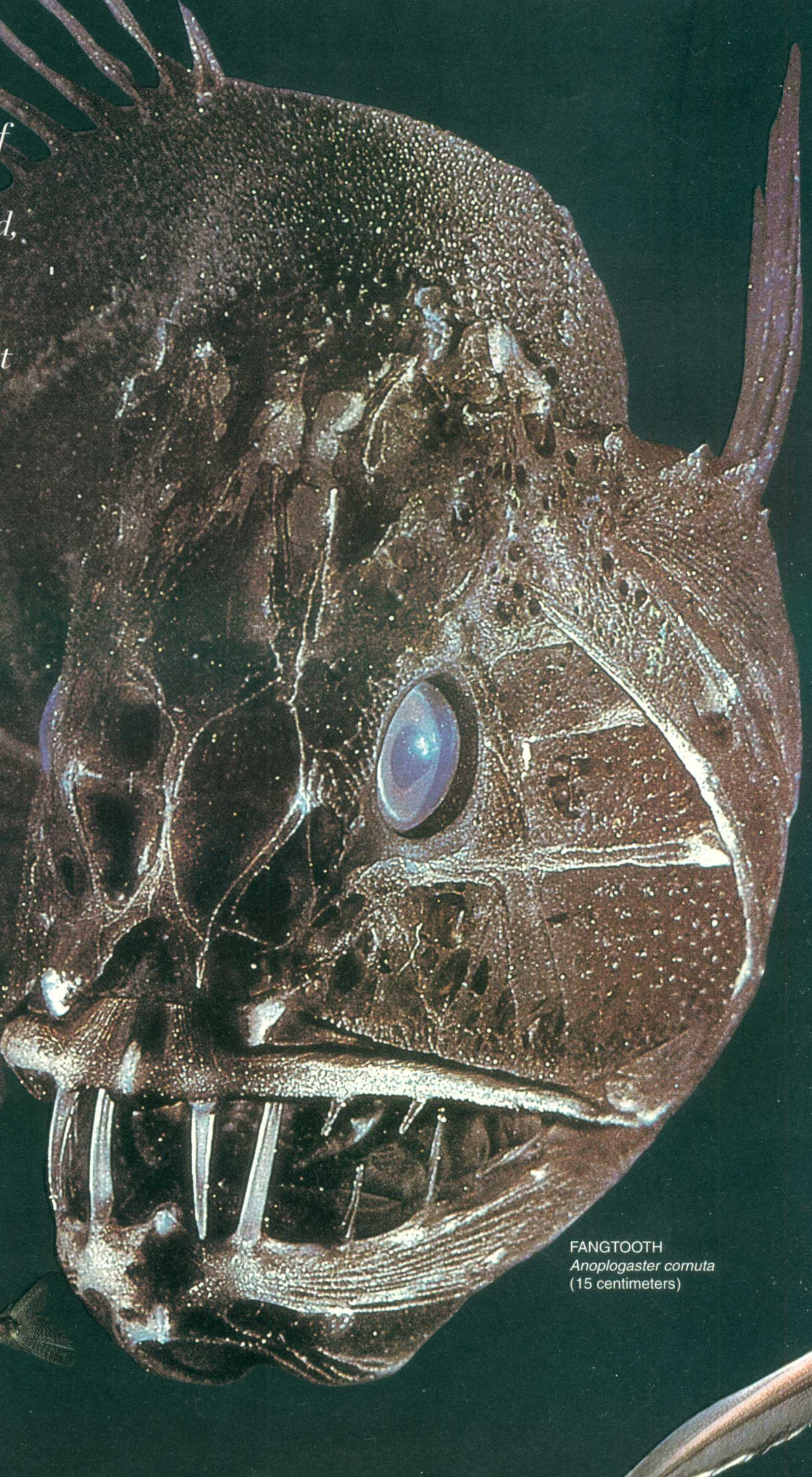
Light in the Ocean's Midwaters

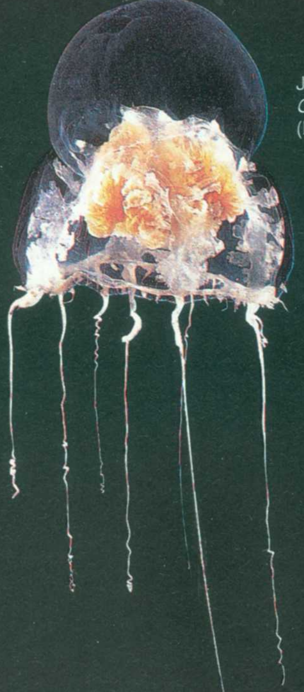
Beneath the surface of the ocean, sunlight is gradually extinguished, but the resulting darkness yields to a host of bioluminescent creatures

by Bruce H. Robison



FANGTOOTH
Anoplogaster cornuta
(15 centimeters)

HATCHETFISH
Sternoptyx diaphana
(2.5 to 9.0 centimeters)



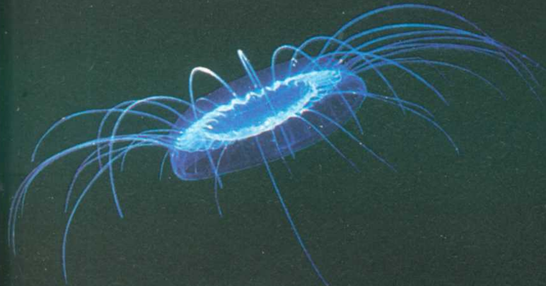
JELLYFISH
Catablema sp.
(Bell diameter: 4 centimeters)

Vampyroteuthis infernalis
(25 centimeters; inverted configuration at right)

DRAGONFISH
Idiacanthus antrostomus
(40 centimeters)

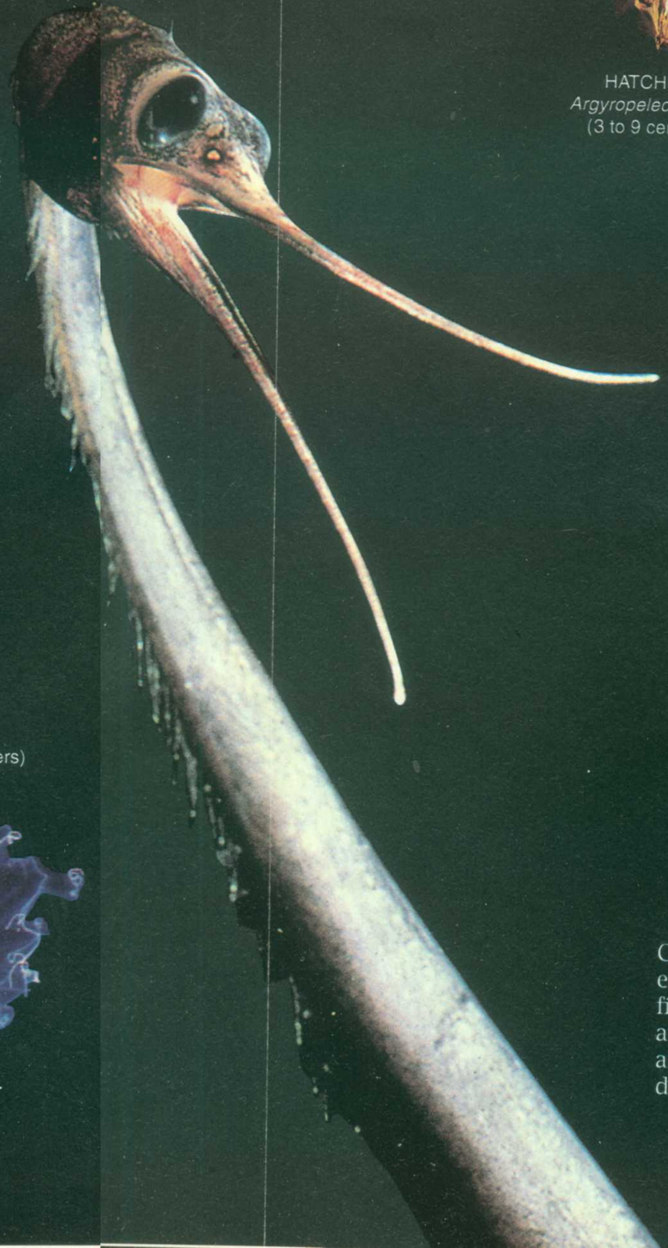
HATCHETFISH
Argyropelecus pacificus
(3 to 9 centimeters)

EELPOUT
Melanostigma pammelas
(5 to 10 centimeters)

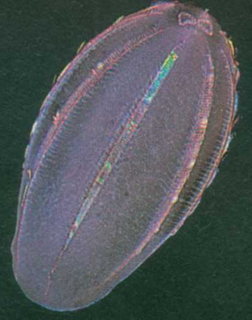


NARCOMEDUSA
Solmissus marshalli
(Bell diameter: 15 centimeters)

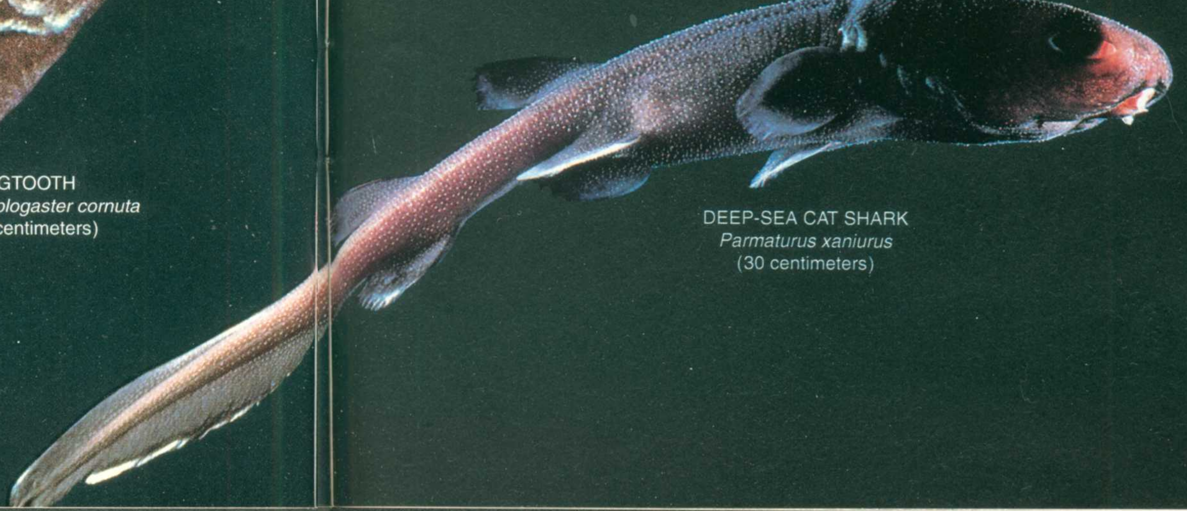
Periphylla periphylla
(Bell diameter: 7 centimeters)



SNIPE EEL
Nemichthys scolopaceus
(1 meter)

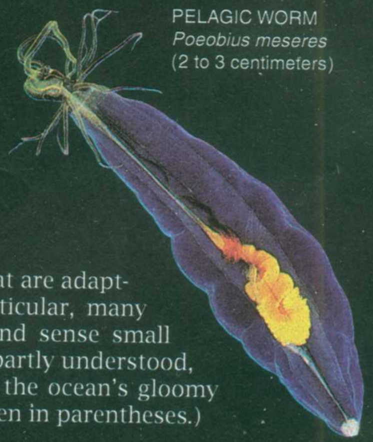


CTENOPHORE
Beroë
(5 to 12 centimeters)



DEEP-SEA CAT SHARK
Parmaturus xaniurus
(30 centimeters)

Colobonema sericeum
(Bell diameter: 2.5 centimeters)



PELAGIC WORM
Poeobius meseres
(2 to 3 centimeters)

CREATURES OF THE MIDWATERS take diverse forms that are adapted to their environment in a variety of ways. In particular, many fishes, squids and gelatinous animals can produce and sense small amounts of light. The role of such illumination is only partly understood, and for many animals it remains a mystery hidden in the ocean's gloomy depths. (Approximate sizes of those shown here are given in parentheses.)

BRUCE H. ROBISON; SEA STUDIOS (jellyfish, pelagic worm, ctenophore); KIM REISENBICHLER (*Vampyroteuthis*)

The most expansive animal habitat on the earth lies between the sea surface and the floor of the deep ocean basins. Within this enormous volume live the largest and perhaps most remarkable biological communities anywhere. Yet because this region is so foreign to the world of normal human experience, we still know extraordinarily little about its fauna. But the quest to understand the nature and behavior of these unfamiliar organisms has been making steady progress. Over the past few years my colleagues and I at the Monterey Bay Aquarium Research Institute in northern California have been able to explore the ocean below the sunny surface waters and to examine local ecology from the novel perspective that modern oceanographic technology affords. And, as is often the case when one gets to view something from an entirely new vantage point, that undersea world looks very different from what we had imagined.

My studies of the biology of the ocean's midwaters—a zone that reaches from about 100 meters to a few kilometers below the surface—have benefited enormously from countless hours spent on board *Deep Rover,* a one-person research submarine. Less adventurously but just as effectively, my work has also taken advantage of a remotely operated vehicle (or ROV) named *Ventana,* a maneuverable, computerized platform about the size of a small car that is fitted with an arsenal of cameras, instruments, sensors and samplers.

These two underwater vehicles boast capabilities that far surpass the relatively crude tools that supported previous midwater research. During the 1950s, for example, the marine biologist Eric G. Barham of Stanford University also examined the ocean near Monterey Bay, but at that time he was limited to using sonar and trawl nets towed behind a ship to identify and track the movements of midwater fauna. In the course of his pioneering studies he uncovered a rather limited set of animals—shrimps, lanternfish, squids and arrow worms—and determined the broad patterns of their vertical migrations, from depths of around 300 meters during the day, up to the surface layers at night.

But with the primitive technology then available, Barham's early research missed a tremendous amount of detail in the ocean simply because he could not view it directly. With *Deep Rover* and *Ventana* my colleagues and I have found that the ocean's midwaters contain a far greater variety of organisms than Barham could possibly have caught in his nets: some forms of sea life are simply too fragile to be extracted from their supportive, watery environment. In many respects, we now think of this delicate marine life as *forming* much of that midwater environment.

Among the larger pieces of biological substratum pervading this region are the bodies of gelatinous animals, along with their extended feeding structures and discarded body parts. The most striking contributions of this kind in Monterey Bay are generated by the elongate siphonophores, linear assemblages that can stretch as much as 40 meters—making them some of the longest creatures on the earth. Whether these animals should be regarded as organized colonies of individuals or as a single, complex superorganism remains unclear. I think of them as living drift nets.

Another part of the biological backdrop common in midwater is composed of the balloonlike feeding filters of animals called appendicularians. The most prominent examples are those produced by the giant form, *Bathochordaeus,* an animal that secretes sheets of mucus that look to an underwater observer like floating islands. Because a multitude of midwater animals regularly cast off feeding structures and other body parts, at times the water can become thick with them.

The best way to visualize the midwater environment might be to imagine a dim, weightless world filled with ragged, three-dimensional spiderwebs. Although my colleagues and I have made a host of surprising discoveries about this wispy realm during our explorations, perhaps the most intriguing result to emerge from these efforts to probe the ocean's darkness has been an appreciation for the role of light.

Life in the Twilight Zone

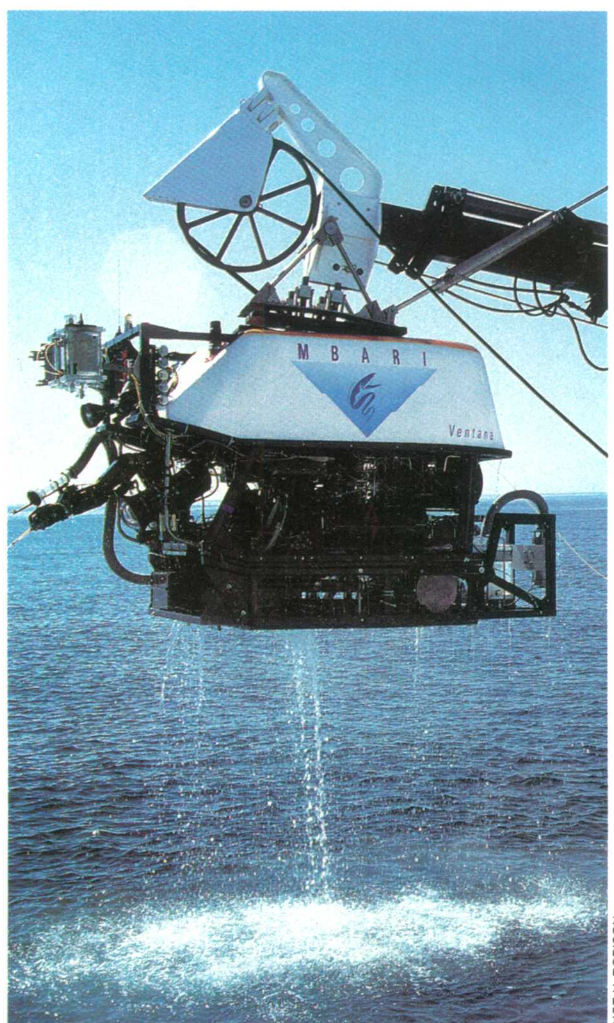
Marine biologists had for decades believed that sunlight could penetrate perhaps 300 to 400 meters below the surface of the sea before it became too weak to support vision—a belief they held despite their knowledge that fishes and squids with large, highly developed eyes lived at depths below these levels. But now that we have been able to observe denizens of supposedly dark parts of the ocean, it is becoming clear that these animals are in fact influenced by the tiny amount of sunlight that does filter down to their abode.

Not until I was able peer directly into this world could I begin to appreciate what the midwater habitat is really like. Submerged alone in *Deep Rover* more than half a kilometer below the surface, I have often switched off the lights of the submarine and looked out at the blackness that surrounds the vehicle's transparent passenger sphere. After letting my eyes fully adjust, I can perceive only that looking up is somewhat less dark than looking down. Yet it has become clear to marine biologists that a variety of animals must utilize this subtle difference. Moreover, we have be-

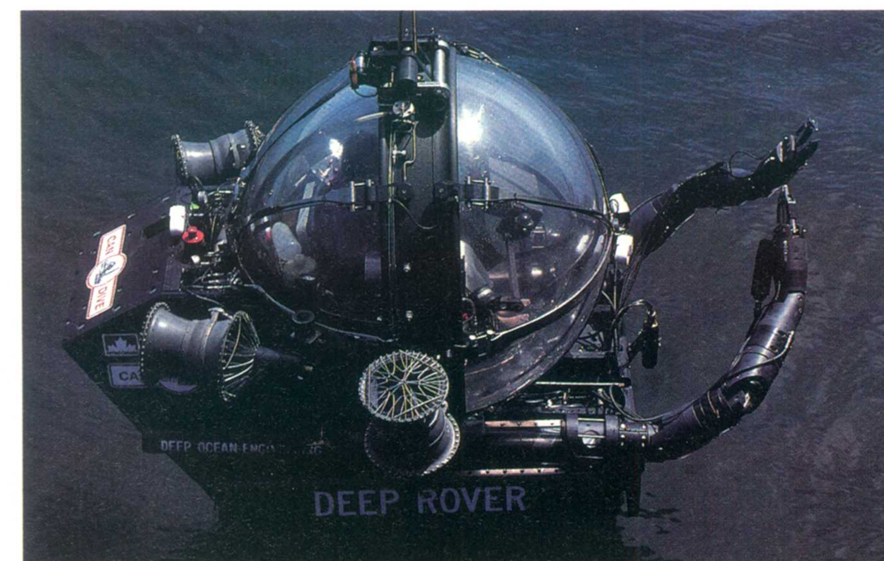
Exploring the Midwaters with Camera and Robot

The submersible *Deep Rover* can carry a single occupant to depths in the ocean as great as one kilometer for up to eight hours at a time. The vehicle's transparent passenger housing—constructed from a massive acrylic sphere 160 centimeters in diameter and 13 centimeters thick—offers the pilot panoramic views of the surrounding waters. The pods underneath the sphere contain banks of lead-acid storage batteries that power the vehicle's lights, electric thrusters and hydraulic manipulator arms, as well as its many other pieces of scientific, navigational and life-support equipment.

In contrast to submersibles such as *Deep Rover, Ventana*—a remotely operated vehicle (ROV)—carries no pilot on board. Instead controllers communicate with the underwater robot through a cable attached to *Ventana's* support ship. Electric power for lights, thrusters and other equipment passes continuously downward through copper conductors within the umbilical tether, and data and video images travel upward, encoded on optical fibers at the core of the cable. Keeping vigil at the monitors of a shipboard console, scientists and pilots control *Ventana's* movements and can, if need be, maintain the vehicle's subsurface research tasks around the clock.



DEEP ROVER submersible vehicle hovers inches above the surface—just before its deployment.



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VENTANA rises from the sea, lifted by a crane on the support ship (*left*). The front of *Ventana's* frame supports cameras, sensors, samplers and a mechanical arm (*bottom center*). Pilot and scientist operate the vehicle together from a control room on board the ship (*bottom right*).

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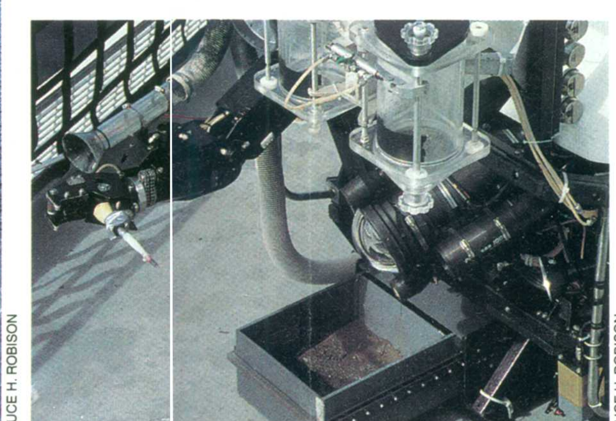

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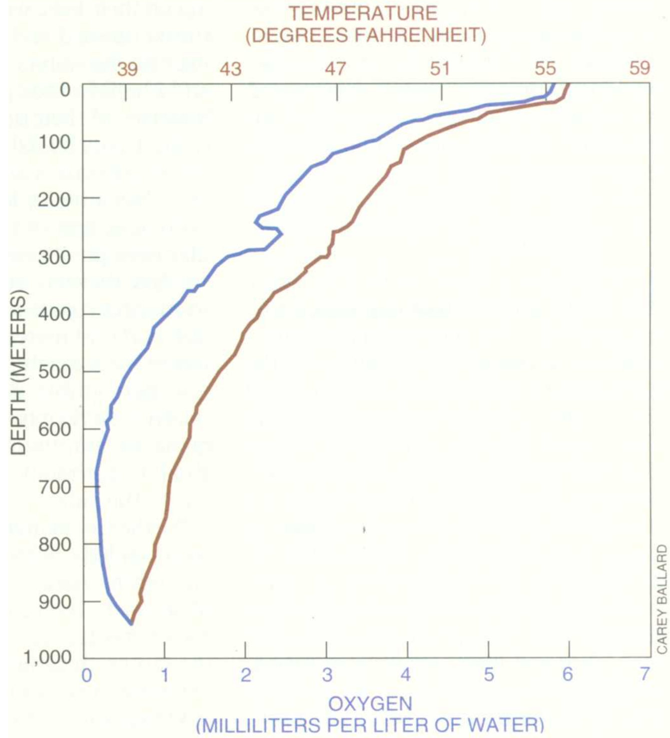
The ROV carries both a black-and-white and a broadcast-quality color video camera. In addition to the two cameras and the powerful video lights, shipboard controllers can employ a scanning sonar system to "peer" into the vehicle's surroundings using high-frequency sound waves. Guided by these devices, scientists are able to make measurements and perform experiments using a variety of special-purpose hardware. These instruments include dye injectors (to track subtle currents), a transmissometer (to measure optical clarity) and a structured light array (to map the density of particulates). The ROV's operators can also capture and recover objects of interest with several types of apparatus. Four detritus samplers, for example, easily encase small but delicate specimens, and a suction sampler is able to draw extended gelatinous animals into the vehicle.

A new ROV called *Tiburon* (Spanish for shark) now under construction at the Monterey Bay Aquarium Research Institute in California should prove even more capable than *Ventana.* Engineers at the institute are also designing and building prototypes of autonomous underwater vehicles. In years to come, these mobile robots will be able to carry out research missions of long duration without the need for a constant human presence—or telepresence—as is now required for operations with *Deep Rover* and *Ventana.*



SIPHONOPHORE deploys an intricate array of tentacles (*above*). If unsuccessful in catching prey, this creature remains in place for only a few minutes before hauling in its elaborate fishing gear and moving to another position. Most animals of the midwaters move effortlessly in three dimensions, but few venture into the anoxic zone near a depth of 700 meters, where oxygen concentration falls to a minimum (*right*).

come keenly aware that most creatures of this twilight world are able to augment the scant sunlight reaching them with another form of natural illumination, bioluminescence.

Although bioluminescence is a relatively rare phenomenon in terrestrial ecosystems, the vast majority of the animals that inhabit the upper kilometer of the ocean are capable of producing light in one way or another. Moreover, much of the particulate matter and biological detritus that floats suspended in these waters will glow after it is physically disturbed. These effects can interrupt the normal blackness of the deep ocean with an eerie light.

Midwater animals employ bioluminescence in myriad ways. Some use it as a burglar alarm, coating an advancing predator with sticky, glowing tissue that makes the would-be attacker vulnerable to other visually cued hunters—like bank robbers marked by exploding dye packets hidden in stolen currency. Others use bioluminescence as camouflage. The glow generated by light-producing organs, called photophores, on the undersides of some fishes and squids acts to countershade them: the weak downward lighting effectively erases the shadow cast when the animal is viewed from below against lighted waters above.

The midwater squids *Chiroteuthis* and *Galiteuthis,* for example, clearly demonstrate this use of bioluminescence. Their bodies are transparent except for their dense eyes and ink gland. Ornate light organs arrayed underneath these opaque structures shine downward to countershade them, whatever the position of the squid—head up, head down, inverted or upright. I have found it a bit unnerving to stare eyeball to eyeball with a creature that can pivot its body around a rigid eye that neither blinks nor changes orientation.

Although marine biologists have been able to understand the usefulness of countershading, other examples of bioluminescence have long eluded our logic. One such enigma is a newly discovered species of tomopterid worm, an active, agile swimmer that has a multitude of paired legs along its tapered body. From specimens caught with nets, biologists have known that some species have structured light organs at the ends of their legs, but only last year James C. Hunt of the University of California at Los Angeles (as well as the Monterey Bay Aquarium Research Institute) and I found a new form of bioluminescent display in a tomopterid that has pigmented pores in roughly the same location as typical leg photophores. This species is a "spewer": when stimulated, it squirts a bioluminescent fluid from each of its leg pores. The discharge forms a luminous cloud that can completely enshroud the body of the worm or leave a glowing trail as it races away. A thimbleful of the ejected fluid contains hundreds of tiny rods that glow brightly yellow. Other types of spewers are known; their strategy may be to cause a visual distraction. But this species remains puzzling. What is the purpose of the display? Why are the tiny light sources rod-shaped? Why is the light given off colored yellow when most midwater animals have eyes that are sensitive only to blue-green?

Another mysterious application of bioluminescence involves much of the suspended particulate matter and most of the larger gelatinous animals living in midwater: they produce light when stimulated mechanically. "Contact flashing" can happen throughout a large volume of this otherwise dim habitat. Most of the time, the surroundings remain tranquil, with abundant flashers at rest in the dark. But the disturbance of driving *Deep Rover* through these depths of the ocean can trigger a barrage of exploding lights. The scene underwater can quickly begin to resemble something out of a *Star Wars* movie.

The natural movements of animals can also cause the ambient biological lighting to turn itself on, and such bioluminescent responses, when they occur on a large scale, can lead to one of the most remarkable sights in midwaters: a propagated display. This phenomenon starts with local motion triggering contact flashers to fire; these bursts then elicit further flashes like an echo through the adjacent water. Previously poised animals begin moving when the background begins to glow, and their wakes in turn stir up even more light. If contact flashing occurs within a layer of dense particles, the cumulative effect of this bioluminescent activity can look like heat lightning rippling through a cloudy summer night. Whatever the motivation for contact flashing among simpler organisms, more highly developed animals of the midwater region seem well adapted to the situation.

Midwater Attackers

Fish such as hake, as well as some squids, are fast-moving, wide-ranging predators, but they often linger near *Ventana*, attracted to the lights of the ROV. It may be that they misinterpret the illuminated waters as an indication that moving prey are present. Perhaps they are conditioned by the daily excursions of sunlight-shunning species that venture near the surface only at night. Such vertical migrations must be light-provoking events, as these animals pass through resident layers of contact flashers. But the potential for movement-induced bioluminescence probably inhibits overall activity, keeping the midwater environment relatively static. Avoiding unnecessary light shows that would give away their position may be the reason mobile animals seem often to remain "parked" in one position much of the time.

Even some predators stay largely motionless. For instance, paralepidids—slender, speedy fish with bodies that look as though they are made of quicksilver—spend the daylight hours standing on their tails, with their sharp snouts thrust upward and their large eyes staring into the waters above. My colleagues and I believe they are searching for silhouettes of their prey against the weakly luminous backdrop. The hatchetfish *Argyropelecus* is another shadow stalker; it has a heavy keel to keep its body horizontal and to stabilize a pair of tubular eyes positioned on top of its body so that its view remains directed upward. *Argyropelecus* lives between about 300 and 600 meters below the surface, where the sunlight must be sufficient to cast perceptible shadows. But a close relative, *Sternoptyx*, lives at depths too great to employ this tactic and has smaller, normally shaped eyes aimed out to the sides.

Further evidence indicates that the weak sunlight of the midwaters is strong enough to guide predators: a diversity of animals living at these depths are transparent. Such a form of appearance (or rather, disappearance) is good protection in this monochromatic, low-light environment. Another optical defense mechanism is red body pigment; this color absorbs the available blue-green light and reflects nothing, a kind of "visual stealth" strategy.

It is not surprising that such optical ploys can work effectively. The visual regime in the midwaters is a bit like the scene from a low-light video surveillance camera. The range of color is narrow; sensitivity is high, but resolution is low; and the directionality of light imparts a flatness to perceptions. To the unaided human eye, the visual field amounts to a coarse pattern of silhouettes and shadows. Within this light-limited milieu there appear to be only four basic shapes: streaks, blobs, strings and spots. Each of these phantoms characterizes a certain kind of subject. Streaks correspond to fishes and squids. Rounded or amorphous blobs are usually gelatinous creatures such as medusae and ctenophores or the weblike feeding structures built from mucus by appendicularians. Stringy material is typically sinking mucus or the tails of siphonophores. Spots can be tiny zooplankton or particles of diffuse organic matter called marine snow.

Within this framework we see a common behavior pattern employed by a variety of creatures. When startled or threatened, some animals change their apparent shape, usually from elongate to rounded. Fishes such as eelpouts curl up into circles and hang motionless in the water. I believe this behavior is a form of mimicry: the animals adjust their appearance to resemble unpalatable objects. From *Deep Rover* I have seen hake strike at fleeing fish while ignoring those that had curled up nearby. The balled-up fish probably resembled medusae—creatures of relatively low nutritional value that deter predators with stinging tentacles. Not all marine biologists agree with this hypothesis, but the observation that this behavior is rarely seen at greater depths (where there is insufficient light for the formation of even rough images) supports the argument for the utility of shape-changing. Such behavior has certainly fooled me at times.

Light for the Blind

Most gelatinous animals, such as medusae, lack eyes and thus cannot form images of any kind. Yet some of these creatures are clearly sensitive to the lights of *Ventana*, even at a distance, showing a mild dislike for the brightness. My colleagues and I are accumulating evidence that suggests this sensitivity to light may regulate the animal's depth during the day. Changing light levels are known to control the morning and evening migrations of fishes and krill, and it would now seem possible that even eyeless creatures may somehow perceive the sun's presence above them.

We documented one example of such light sensitivity during an encounter with an animal called *Bathyphysa*. This bizarre creature, which is about two meters long, has appeared in front of *Ventana*'s cameras only once, while the vehicle was cruising 500 meters below the surface. When the ROV approached it, the stem of the animal was vertical, with its gas-filled "pneumatophore" uppermost. The stem of the *Bathyphysa* had a mane of elongate, serial stomachs (so-called gastrozooids), each with a probing mouth at its end, and all were writhing like snakes. Several five- to 10-meter-long feeding tentacles radiated out from a round, contracted part of the stem at its center. The stem was exceptionally elastic, a trait that seemed to be explained when we discovered the animal's escape response. Sensing the lights of the ROV, this creature began a series of pounding contractions and relaxations of the upper stem that had the effect of driving the animal downward. In concert with these pulsations, gastrozooids were cast off and left to drift away, one at a time. The result was a determined descent, although a fairly slow and taxing one.

Such episodes suggest that eyeless creatures might well be able to sense even low-level light. In any case, it is clear that they can generate it. *Colobonema*, for example, is a beautifully iridescent little medusa that has a "bell" that is about the size of a coin. In the lights of the ROV, muscle bands in the bell have a blue-green metallic sheen. The medusa's tentacles show a deep blue along their length and brilliant white at the tips.

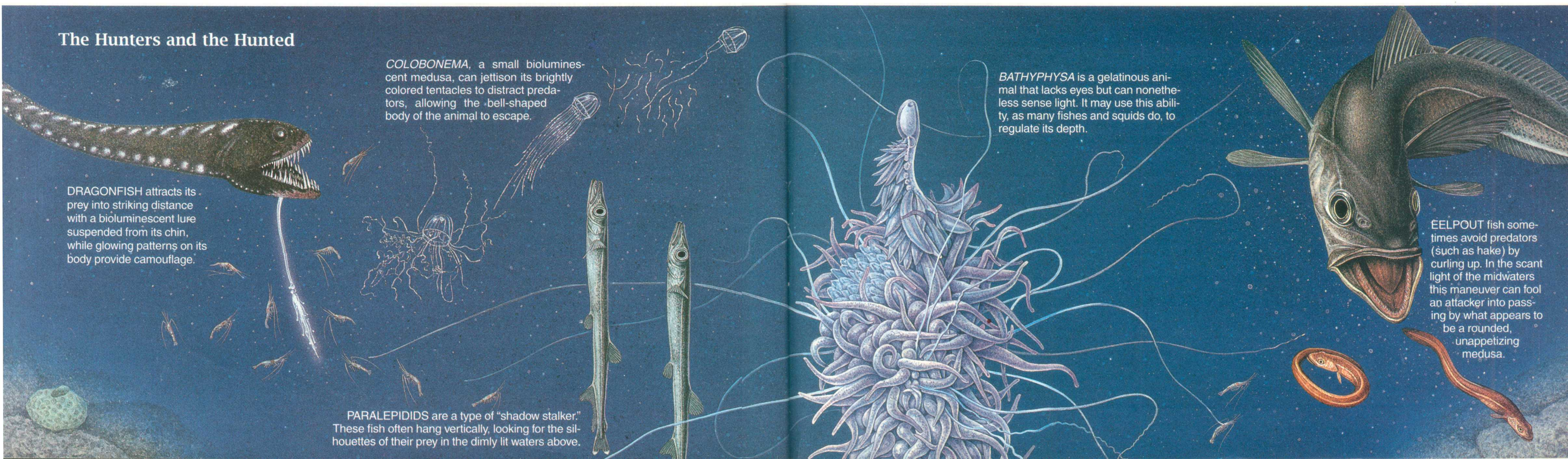
A fully developed individual has 32 tentacles arrayed uniformly around the base of the bell. Often, however, specimens show fewer appendages set in tiers of different lengths. This appearance is perhaps explained by the animal's behavior: when startled, *Colobonema* darts away, leaving a group of bright, swirling tentacles in its wake. From *Deep Rover* I have observed that the release is occasionally preceded by ripples of luminescence pulsing rapidly through the bell. The many tentacles are then dropped as the bell goes dark and zigzags away into the surrounding blackness.

Occupants of the Oxygen Minimum

One of the characteristic features of the Pacific Ocean near Monterey Bay is a zone that is depleted in dissolved oxygen. Just below the sea surface, oxygen concentrations are close to saturation (that is, the water holds as much oxygen as can possibly be dissolved), but deeper in the ocean, oxygen content diminishes. At about 700 meters of depth, oxygen concentration falls to a value that is only one thirtieth of that near the surface. Below this level is a sharp transition from relatively clear water to a milky layer of very small particles. The milky layer shows a moderate amount of oxygen, and at 1,000 meters the concentration rises further. Within the zone of lowest oxygen near 700 meters resides a unique group of animals that have adapted to meet the physiological challenges of near-anoxia.

One of the most curious inhabitants of the oxygen minimum is the archaic

ROBERTO OSTI



The Hunters and the Hunted

DRAGONFISH attracts its prey into striking distance with a bioluminescent lure suspended from its chin, while glowing patterns on its body provide camouflage.

COLOBONEMA, a small bioluminescent medusa, can jettison its brightly colored tentacles to distract predators, allowing the bell-shaped body of the animal to escape.

PARALEPIDIDS are a type of "shadow stalker." These fish often hang vertically, looking for the silhouettes of their prey in the dimly lit waters above.

BATHYPHYSA is a gelatinous animal that lacks eyes but can nonetheless sense light. It may use this ability, as many fishes and squids do, to regulate its depth.

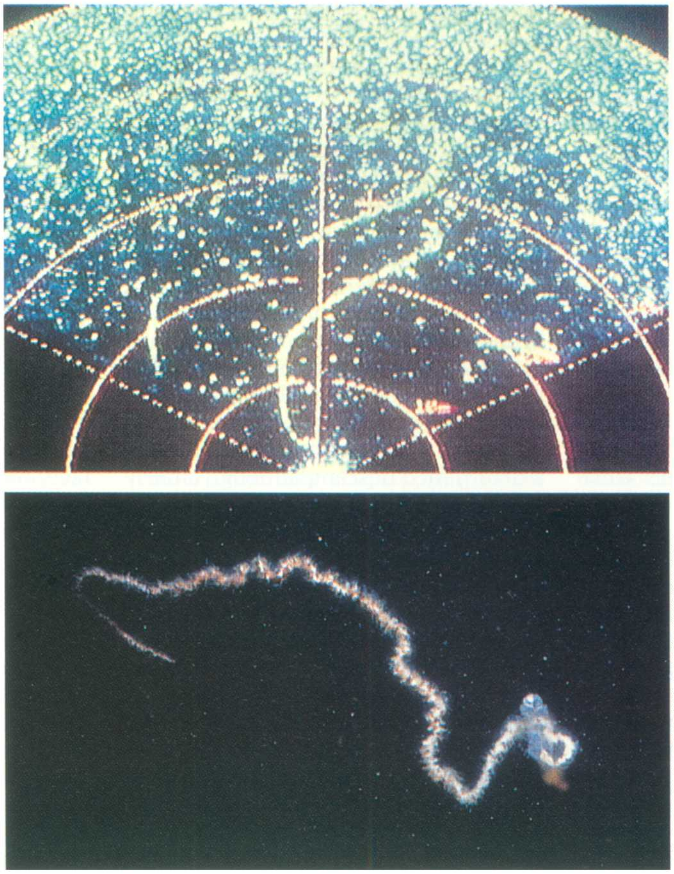
EELPOUT fish sometimes avoid predators (such as hake) by curling up. In the scant light of the midwaters this maneuver can fool an attacker into passing by what appears to be a rounded, unappetizing medusa.

cephalopod *Vampyroteuthis infernalis,* a distant cousin to octopus and squid. A big *Vampyroteuthis* has the size and shape of a soft football. Its body is velvety brown with large eyes that glow like blue opals in the ROV lights. Near the tip of the stubby, conical mantle are two rounded fins and two large light organs with irislike shutters. *Vampyroteuthis* has eight arms like an octopus, but they support a broad web between them. In addition to having suckers, the arms bear a series of paired, fingerlike protrusions, called cirri, that project inward. *Vampyroteuthis* also has two additional appendages: long, elastic sensory filaments that withdraw into pockets between the third and fourth arms on each side.

This creature can be regarded as a living fossil, a modern-day representative of the cephalopods that preceded the evolutionary split into eight- and 10-armed groups. *Vampyroteuthis* propels itself with jets of water expelled from its siphon and by flapping its stubby fins. At the center of the webbed arms is a dark, hooked beak. We do not yet know what this animal eats, but it substantially reduces its own chances of being consumed by living in an inhospitable, anoxic part of the ocean.

My colleagues and I have discovered that this strange animal has a bioluminescent organ at the tip of each of its arms. *Vampyroteuthis* somehow uses these light sources by swinging its webbed arms upward and over the mantle, which turns the suckers and cirri outward and changes the animal's likeness from a football into a spiky pineapple with a glowing top.

This maneuver covers the animal's eyes, but the webbing between tentacles is apparently thin enough for it to see through. We have observed this transformation frequently but remain at a loss to explain exactly what function this unusual behavior might serve.



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APOLEMIA, **an elongate gelatinous creature (*bottom*), may be regarded as either a colonial animal or a superorganism. A sonar scan of such "living drift nets" (*top*) has semicircular reference lines at 10-meter increments and shows that some of these organisms can extend up to 40 meters, making them among the longest animals known.**

Technology-Driven Exploration

The present length of *Ventana's* umbilical tether has permitted us to explore a volume of water one kilometer deep with a visual resolution that extends from about one centimeter to several hundred meters. Although this span covers the ranges of a large portion of the region's midwater species, there are still many measurements we cannot yet make. But this situation is changing. Future technical development by engineers at our institute should allow us to probe even deeper. Soon new optical and acoustic sensing systems will let us examine larger volumes from greater distances and so allow us to assess the distribution of midwater animals even more thoroughly.

We expect eventually to have autonomous probes that will leave time-lapse cameras in place so that we can track slowly moving animals around the clock for days at a time. Fast-swimming robotic vehicles will follow mobile animals, allowing us better to observe their feeding and migration patterns. The possibilities for investigation seem endless. Hence, despite the numerous discoveries already made, we must consider our undersea investigations to have just begun—the ocean's depths are so vast, and there is so much more to explore.

The Author

BRUCE H. ROBISON developed his curiosity about the ocean early, growing up on the beach in southern California. After receiving a B.S. from Purdue University and an M.A. from the Virginia Institute of Marine Science, he returned to his home state to attend Stanford University, where he completed a Ph.D. degree in 1973. Robison then spent two years in postdoctoral training at the Woods Hole Oceanographic Institution in Massachusetts before taking a position at the University of California, Santa Barbara. In 1987 he joined the fledgling Monterey Bay Aquarium Research Institute in Pacific Grove, Calif., where he is currently a senior scientist and science department chair. Robison's research in deep-sea ecology has carried him throughout the Pacific, to the Atlantic and to the great Southern Ocean surrounding Antarctica. He led the first team of scientists trained as submersible pilots and has long been active in promoting advanced undersea vehicles for oceanographic research.

Further Reading

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