Frogfishes

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# Frogfishes

*Masters of aggressive mimicry, these voracious carnivores can gulp prey faster than any other vertebrate predator*

by Theodore W. Pietsch and David B. Grobecker

On the morning of December 29, 1696, a Dutch captain and his crew were searching for the survivors of a ship that had gone down not far off the coast of Western Australia. Although no survivors were ever found, what the crew did find washed up on the shore of a nearby island—amid rats as big as house cats—was a most remarkable fish. The fish, unlike any the sailors had ever seen, was described as being "about two feet long, with a round head and a sort of arms and legs and even something like hands." There is no doubt in our minds (although its specific identity will never be known) that this strange fish—sketchily described so long ago—was a frogfish.

Aptly named, these unusual fishes do bear a surprising resemblance to frogs: their bodies (which range in length from one to 16 inches) are globose and equipped with well-developed leglike fins that enable them to clamber across rocks, sand and coral reefs, much as a tetrapod might move about on land. They occur in nearly every imaginable color and can alter their hue to match a background object, such as a piece of coral, within a matter of days (in some species within a matter of seconds). As a result, a frogfish that moves from one type of substrate to another can change its color and still blend in with its surroundings. For that reason, most frogfishes are virtually impossible to distinguish from their backgrounds, and so many are overlooked—not only by their predators but by experienced divers and ichthyologists as well.

Commerson's frogfish, *Antennarius commersoni*, which is widespread in the Indian and Pacific oceans, is representative of the group in many ways. Males and females occur in a wide range of colors (including red, yellow, brown, creamy white, black and various hues in between); their skin, moreover, is accentuated by a regular pattern of small brown spots and pink blotches. In shallow water, where streaks of sunlight mottle the ocean floor, the fish bears a remarkable—almost uncanny—resemblance to an algae-encrusted rock. And there it sits, the classic example of a lie-in-wait predator, ready to strike at any fish or crustacean that passes by. Should a suitable animal swim too close, the large, cavernous mouth of the frogfish opens, engulfing its hapless victim in a matter of milliseconds.

Mastering the art of mimicry has thus imbued frogfishes with an important evolutionary advantage. By appearing to be inanimate, frogfishes are not only overlooked by those that prey on them, but they are also overlooked by their own prey. In addition, they are surprisingly effective at enticing prey within striking distance—in large part because they possess a small appendage called a lure that projects forward from just above the animal's lip and can be wiggled when prey come into view.

As long ago as 344 B.C., Aristotle remarked on the role of the lure: "The fishing-frog has a set of filaments that project in front of its eyes; they are long and thin like hairs...and are used as baits." Those observations were reconfirmed in 1875 by the Reverend S. J. Whitmee of Samoa, who described angling in a frogfish: "It angled...for

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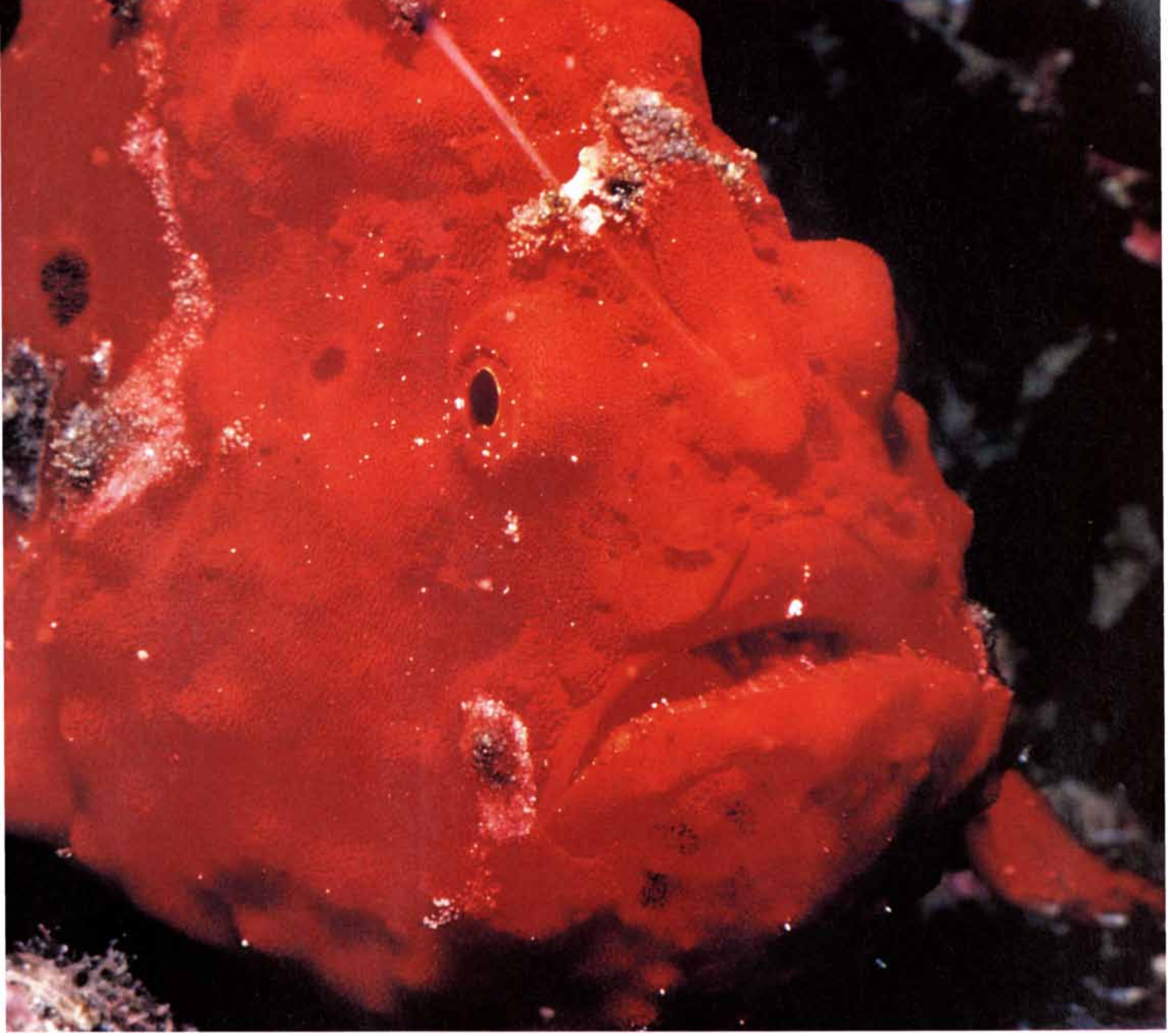
***PAINTED FROGFISH,* Antennarius pictus, *lives in the warm shallow waters surrounding the Hawaiian islands. Like***



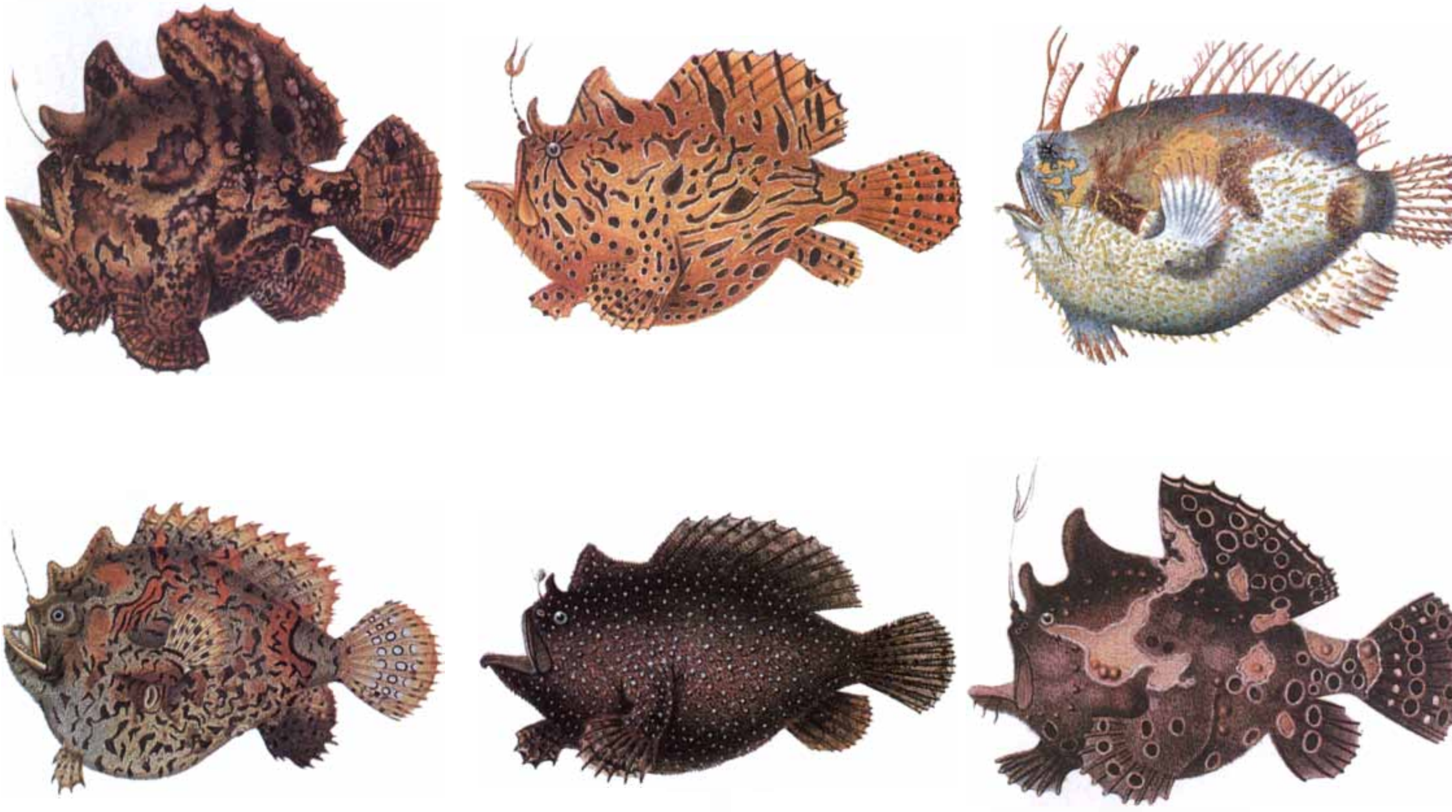
***all frogfish species, it attracts prey by wiggling a lure, which is a modified, elongated dorsal-fin spine. The lure, seen here extending diagonally upward between the fish's eyes, terminates in a structure called the esca, or bait. Animals that are attracted to the lure and come too close to the cavernous mouth of the frogfish are engulfed in a matter of milliseconds.***

some of the small fish in the aquarium. I hoped to see it catch one; but they were too wary."

Whitmee's observations, which were later substantiated by others, represent a concept in behavioral biology that is known today as aggressive mimicry. Unlike passive mimicry (whereby camouflage, or resemblance to one's background, provides a certain degree of protection from one's predators), aggressive mimicry requires that an animal imitate a specific object, both physically and behaviorally, in order to gain some advantage from it. In other words, by mimicking not only an inanimate object but also the behavior and appearance of a particular food item, a frogfish can lure another animal into its strike zone. Studies we have carried out now indicate that the frogfish, with its wide array of specialized adaptations, is one of nature's best (most highly evolved) examples of aggressive mimicry.

Frogfishes belong to the family Antennariidae, which in turn belongs to a larger assemblage of bony fishes, the anglerfishes. As the name implies, anglerfishes are largely sedentary, lie-in-wait predators that attract prey with the aid of a lure. In the case of frogfishes, the lure—a highly conspicuous extension of the first spine of the dorsal fin—sways forward from the face, imitating the jigging action of a fisherman's rod. In some species the entire apparatus can be folded back into a narrow groove on top of the head, and thus, the lure is protected when not in use.

Lures, which vary from species to species, consist of two major parts: the spine itself and a conspicuous fleshy structure at the tip called the esca, or bait. Depending on the species, the



***FROGFISHES belong to a large and diverse family (the Antennariidae) as the above drawings—which were made more than 100 years ago—indicate. From left to right at the top, the species shown are Commerson's frogfish* (Antennarius commersoni)*, the striated frogfish* (Antennarius striatus)*, the tasseled frogfish* (Rhycherus filamentosus) *and the painted***

esca may range in size and shape from a simple ball of tissue, perhaps 1/16 of an inch in diameter, to a highly ornate and filamentous structure an inch or more in length. In some species the esca mimics a small fish; in others it seems to mimic a crustacean or a worm.

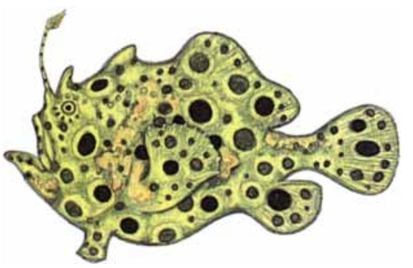
Although widely distributed in tropical and subtropical waters around the world, including the Gulf of California and the Red Sea, the vast majority of frogfishes are confined to the coastal areas of Indonesia, the Philippines and various other island groups of the South Pacific. One species, *Histrio histrio,* lives amid floating sargassum weed; the remainder spend their lives either on the ocean bottom (in areas where the water is shallow to moderately deep) or on rock or coral reefs.

Most taxonomists now agree that there are about 41 known species of frogfishes, although as many as 165 have been formally described over the past century or two. Such taxonomic confusion can be blamed in part on the amount of variation in both color and pattern that occurs within a single species.

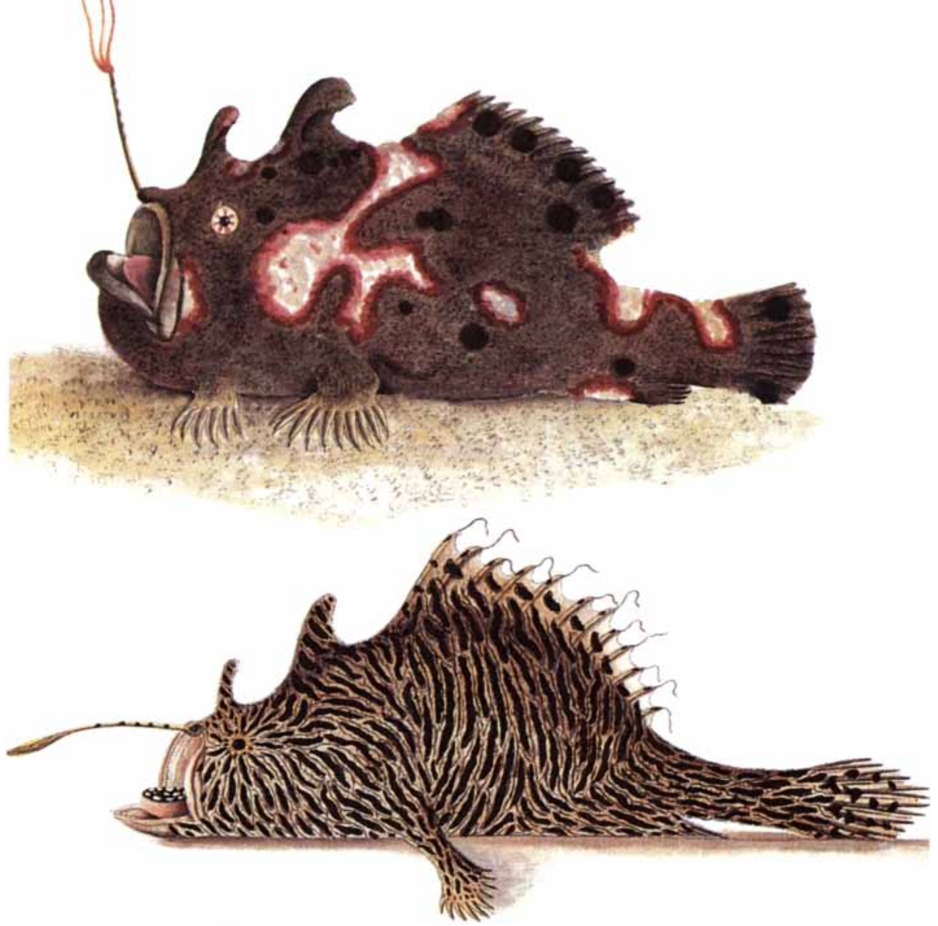
Individuals have the ability to switch back and forth between two color phases: a light phase (usually yellow or tan) and a dark phase (often green, dark red or black). Although the light phase seems to predominate in most habitats (for reasons that are not well understood), it is not uncommon to find an area where the entire color range for the species is represented.

The striated frogfish, *Antennarius striatus*, for example, maintains at least four distinct color phases: a green phase, during which it looks very much like an algae-covered rock; an orange phase, during which it has the appearance of an orange sponge; a white phase, during which it seems to mimic a white sponge; and a black phase, when it is reminiscent of a black sponge. We surmised that such marked change in color must occur when the fishes move to a slightly different habitat—say, a region of the coral reef where orange sponges rather than white ones predominate.

In order to test the response of frogfishes to background visual cues, we devised an experiment involving two species: the tuberculated frogfish, *Antennatus tuberosus,* and Commerson's frogfish, *A. commersoni*. We placed individuals in separate observation tanks and after a period of habituation changed the color of the gravel substrate (from white to black) and also added rocks and coral in various color combinations to the tank. Although the tuberculated frogfish changed from dark gray to light cream and Commerson's frogfish changed from lemon yellow to brick red, we were unable to determine the precise stimuli responsible for the color transformation. Clearly, further studies under natural field conditions are necessary.



***VARIATION IN PIGMENTATION can be quite marked within a single species of***



***frogfish* (Antennarius pictus)*. From left to right at the bottom, they are the three-spot frogfish* (Lophiocharon trisignatus)*, the New Guinean frogfish* (Antennarius dorehensis)*, the warty frogfish* (Antennarius maculatus) *and the striated frogfish.***

We do know that the frogfish is a voracious and highly successful predator. Not only is it virtually indiscriminant in its dietary preferences, but it will attempt to swallow anything within striking distance, including animals slightly bigger than itself. By studying the feeding behavior of frogfishes, we have determined, for example, that a frogfish can enlarge its mouth by a factor of 12; moreover, it can do so in about six milliseconds—less time than it takes for a normal striated muscle to contract. We have also analyzed locomotion in these fishes, which ranges from "walking" across the substrate to jet propulsion.

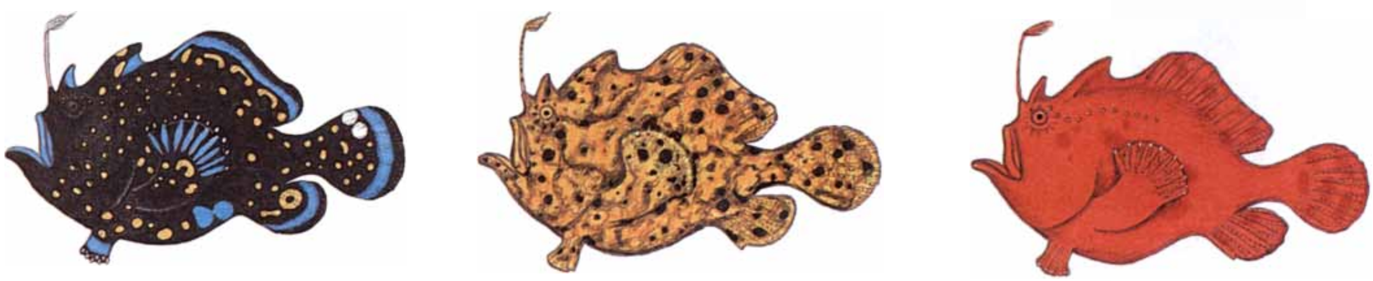
Our studies, which have been carried out both in the laboratory and at field sites off the coast of Oahu, Hawaii, and in Sydney Harbor, Australia, during the past 15 years, have enabled us to amass varying amounts of behavioral and ecological data for eight different species: Commerson's frogfish, the striated frogfish, the tuberculated frogfish, the hispid frogfish (*A. hispidus*), the warty frogfish (*A. maculatus*), the scarlet frogfish (*A. coccineus*), the bloody frogfish (*A. sanguineus*) and the three-spot frogfish (*Lophiocharon trisignatus*).

We began our research by analyzing luring behavior; in particular, we wanted to know whether luring directly influences the kinds of prey that a frogfish captures. Are lures species-specific, that is, does each species of frogfish have a morphologically unique lure? And is there a correlation between the appearance of the lure and diet, that is, does the lure resemble the preferred food items of the species attracted to it?

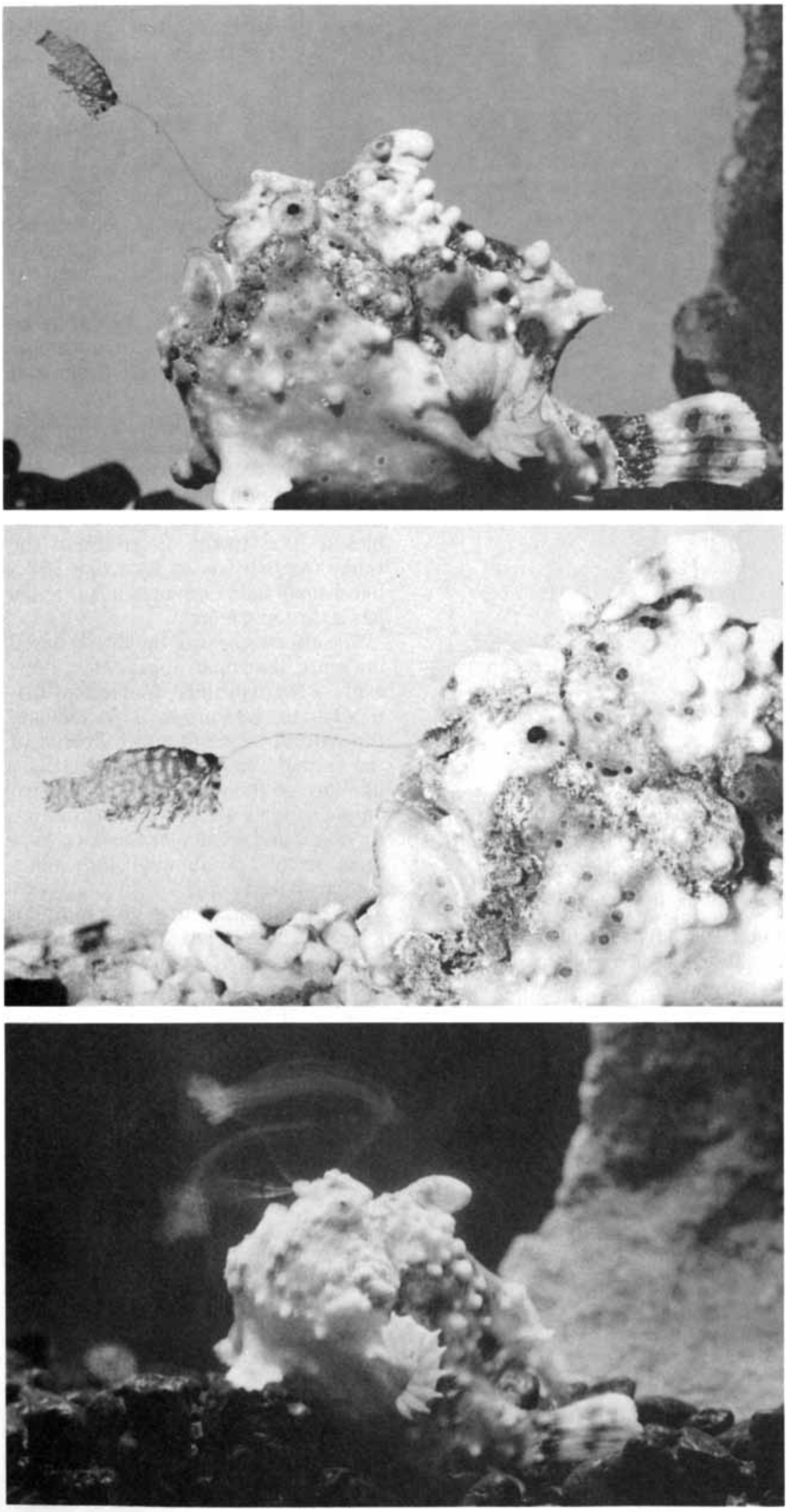
The shape and size of the lure, it seems, are unique to most species; in fact, a species can often be identified on the basis of its lure alone. The esca of the striated frogfish looks something like a polychaete worm, whereas the esca of the hispid frogfish resembles a tube worm. In contrast, the warty frogfish has an esca that looks like a small fish; Commerson's frogfish has a shrimplike one.

The effectiveness of the lure is based on more than just appearance, however. A frogfish must wiggle and manipulate the lure in ways that simulate the natural swimming movements of the animal being mimicked. The fishlike lure of the warty frogfish, for example, ripples as it is pulled through the water and so mimics the lateral undulations of a swimming fish [*see illustration on next page*].

We hypothesized that such morphologically distinct lures might reflect a highly specialized diet. After all, it seemed reasonable to suppose that a striated frogfish, with its wormlike esca, might feed primarily on species that normally prey on (and are therefore most attracted to) polychaetes or other marine worms. To test our hypothesis, we decided to analyze the stomach contents of four species: *A. striatus, A. pictus, A. commersoni* and *Antennatus tuberosus*. Somewhat to our surprise, our study revealed that frogfishes are not specialized feeders



***frogfish. It is thought that individuals change color to mimic particular objects in their environment, such as rocks, sponges or pieces of coral. Only four (of many) color and pattern phases of the painted frogfish,* A. pictus*, are shown here.***



*APPEARING TO MIMIC its background, in this case an algae-encrusted rock* (top)*, the warty frogfish,* A. maculatus*, sits for hours waiting for potential prey to swim by. The tip of the lure (called the esca) varies from species to species, but here it resembles a small fish* (middle)*. If another animal comes into view, the frogfish wiggles its lure* (bottom) *in a way that mimics the movements of a small fish.*

but eat a highly varied, overlapping assortment of prey.

Our findings were unexpected. Why, we wondered, should evolution favor such complex and apparently species-specific lures when the average frogfish is successful at attracting a wide variety of prey? One possible explanation is that food acquisition in the marine environment is both unpredictable and complex. Many individuals will randomly enter a frogfish's strike zone without being specifically attracted to the lure; others are attracted to the area not by the wriggling lure but by the frogfish itself, which may be mistaken for an appropriate site (such as a piece of coral) on which to lay eggs, graze or seek shelter.

Another possibility is that the lure may elicit a defensive or territorial response from nearby fishes. In a laboratory experiment involving the damselfish, *Dascyllus aruanus*, we observed that individual damselfish placed in the same tank as a frogfish would repeatedly direct aggressive displays toward the lure. On several occasions, in what seemed to be an overly aggressive attack, a damselfish entered the strike zone of the frogfish and was eaten.

Capture under those circumstances is instantaneous; indeed, almost any fish that swims within the strike zone (an area whose radius is roughly two thirds the length of the frogfish) has little chance of survival. To our knowledge, a frogfish can extend its mouth and engulf its victim at a speed greater than that of any other vertebrate predator. In fact, such rapid prey capture is perhaps the most remarkable of all the frogfish's attributes.

With the aid of such modern techniques as high-speed cinematography, we have spent a considerable amount of time analyzing the biomechanics of feeding in three species: *A. striatus*, *A. hispidus* and *A. maculatus.* By integrating frame-by-frame analyses of high-speed film (from 800 to 1,000 frames per second) with anatomical analyses of the bones, muscles and ligaments in the fish's head, we have come to realize that prey capture in the frogfish involves a highly choreographed sequence of behaviors.

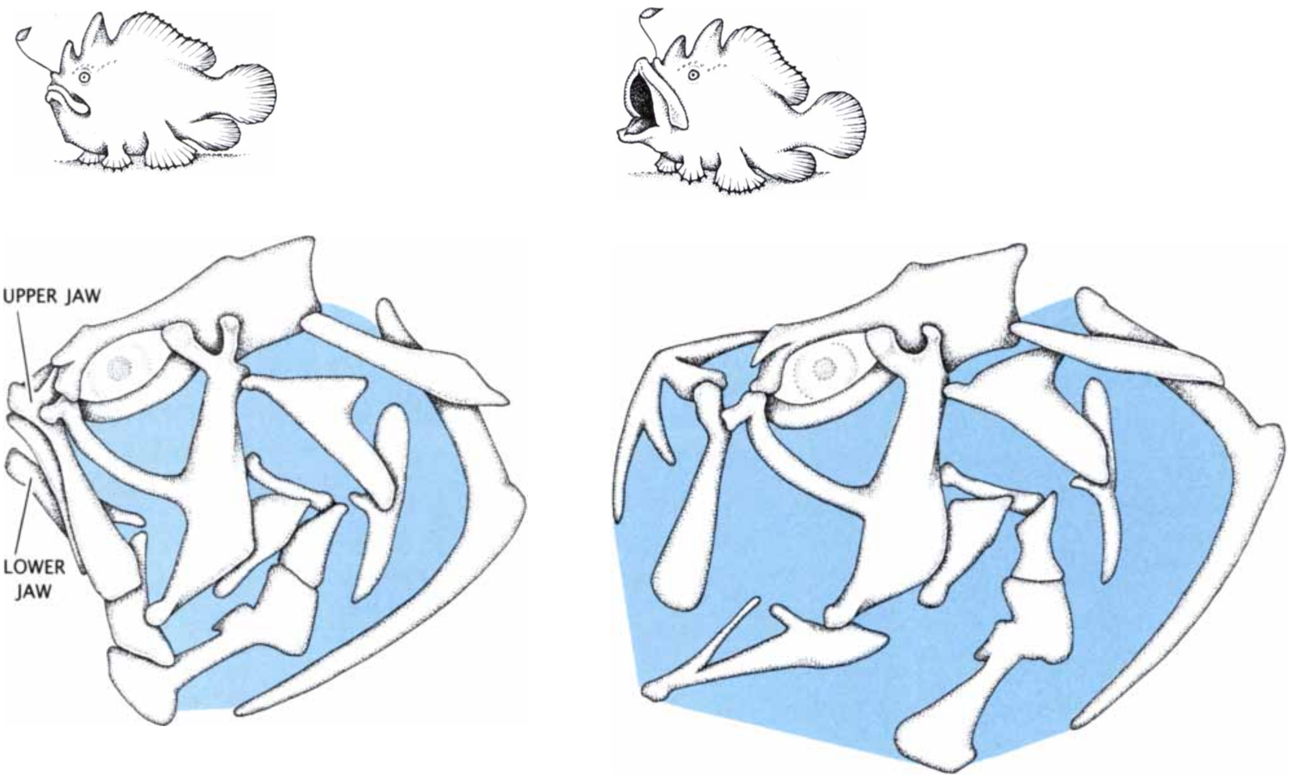
Three functionally distinct phases can be identified. Phase one consists of prestrike behavior, phase two is the strike itself and phase three is prey manipulation, which involves swallowing. During the prestrike phase, prey are followed visually until they come within a certain distance (about seven body lengths) of the frogfish. At that point, the frogfish begins wiggling its lure. If

*RADIOGRAPH shows that the longlure frogfish,* **A. multiocellatus,** *has swallowed a scorpion fish* **(Pontinus** *sp.), which is longer than itself. A frogfish can swallow such large prey because its mouth expands in size by a factor of 12 or more.*

the prey responds by approaching the lure, the frogfish then enters the strike phase. If the prey does not respond, the frogfish may start moving toward it—rapidly at first but then much more slowly. During the slow phase the frogfish flattens its body into what looks like a crouching position; doing so presumably renders it less conspicuous to its victim. When the targeted prey is about one body length away, the frogfish (now in the strike phase) orients itself by twisting or rocking its body into the proper position for attack.

The frogfish waits for the prey to enter its strike zone and then lifts its head and opens its mouth by depressing the lower jaw at the same time that it expands the upper jaw. In that configuration, the mouth forms an extended tube, which sucks a victim inward in much the same way that a vacuum cleaner pulls dust from a carpet. Once the prey is taken into the mouth, the frogfish enters the prey-manipulation phase. As the prey is swallowed, a large quantity of water is also ingested, which facilitates the passage of large prey into the frogfish's gullet. When swallowing is complete, excess water is ejected through the gills and a sphincter muscle at the base of the esophagus closes, which prevents the prey from escaping.

This method of prey capture, which is practiced by most of the world's fishes, is known as gape-and-suck feeding. The underlying principle is a simple one: negative pressure (suction) is created by the rapid expansion of the gill cavity and mouth, which creates an inward flow of water and so increases the speed with which prey are engulfed. Unlike fast-swimming predators that incorporate body speed to engulf prey, the lie-in-wait predator depends on the rapid expansion of its oral cavity in order to surprise and capture its prey. The gape-and-suck predator can also feed on prey without advertising its presence to other potential prey. Fish in close proximity to one another, for example, are often apparently unaware of the sudden loss of one of

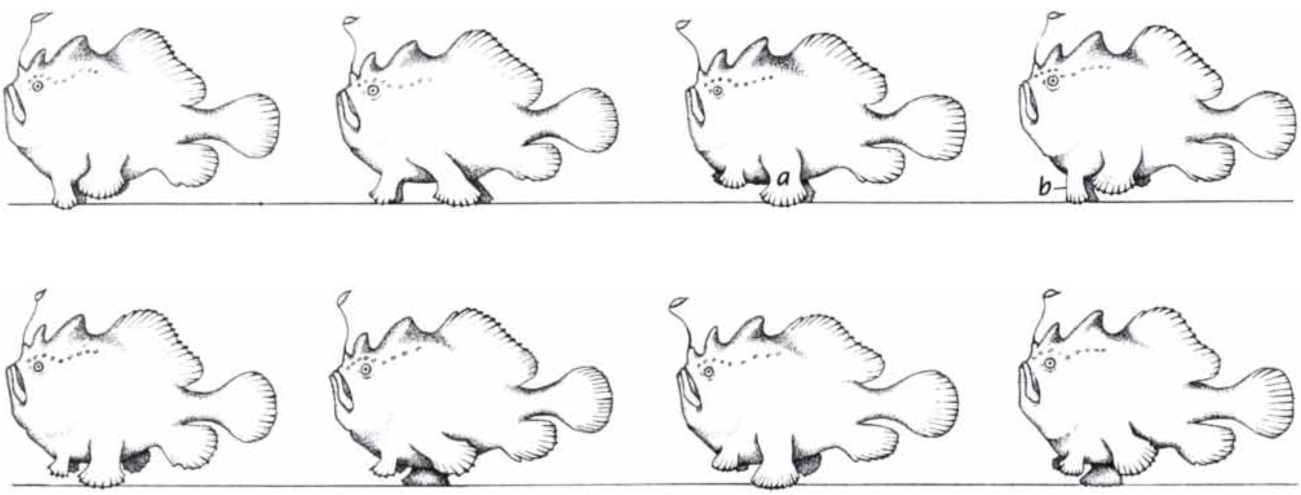



*FROGFISH'S MOUTH remains closed* (left) *until suitable prey comes within striking distance. The frogfish then contracts the muscles of its upper and lower body and throat, which causes the head to lift and the mouth to open* (right)*; these same muscle contractions cause the upper jaw to push outward and the lower jaw to descend. As the mouth expands, it extends forward (a process that takes about six milliseconds), which enables the frogfish to suck in its victim.*

their neighbors and so remain vulnerable to repeated strikes by a lie-in-wait carnivore.

The difference between frogfishes and other fishes is the degree to which the mouth expands as well as its rate of expansion. We have determined, by injecting liquid paraffin into both the closed and fully expanded mouths of preserved fishes, that frogfishes can expand their mouths to a much greater extent than other gape-and-suck feeders. The European perch, *Perca fluviatilis*, for example, expands its mouth by only a factor of six when feeding.

Moreover, the frogfish's mouth expands with incredible rapidity. Analyses of high-speed films indicate that the hispid frogfish opens its mouth and engulfs its prey in less than six milliseconds. Similar times were meas-




*FROGFISHES MOVE across the substrate with the help of leglike fins. They do so either by "crutching"* (top) *or by "walking"* (bottom)*. When crutching, the fish moves forward by resting its weight on the pectoral fins* (a)*; the pelvic fins* (b) *bear the animal's weight only while the pectoral fins are being repositioned. When walking, the frogfish alternates its pectoral fins, pushing forward first with one, then the other, much as humans move their legs when walking.*

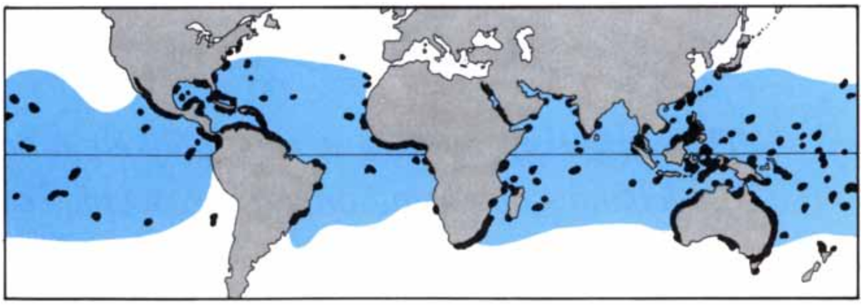
ured for the striated and warty frogfishes. By comparison, the stonefish, *Synanceia verrucosa,* which is thought to be the next fastest gape-and-suck feeder, requires 15 milliseconds, and the European perch needs a full 40 milliseconds.

We wondered about the mechanism that makes such speed possible. Do frogfishes have specially modified jaws? A unique set of muscles? What accounts for their remarkable prey-capturing ability? To answer those questions, we dissected the heads of several species and carefully examined the muscles responsible for opening the jaw. Our results were unexpected: there are no significant structural differences between the jaw muscles of frogfishes and those of other vertebrates. Moreover, we found no significant differences in bone structure.

Although we have yet to determine the means by which frogfishes open their mouths so quickly, we suspect that a currently unknown mechanism may be responsible. Perhaps frogfishes possess a biomechanical feeding mechanism similar to the mechanism in fleas that enables them to store elastic energy in the thorax and so jump to incredible heights [see "The Flying Leap of the Flea," by Miriam Rothschild et al.; SCIENTIFIC AMERICAN, November, 1973]. Is it not possible that frogfishes have a catapault mechanism in the jaw that enables them to store elastic energy and then quickly release it? We think such a modification may exist, although further studies are needed to confirm our hypothesis.

The family Antennariidae enjoys many other highly complex and fascinating adaptations, including novel forms of locomotion. To move across the substrate, either in pursuit of prey or in search of a new resting site, frogfishes rely on one of two tetrapodlike gaits. One is reminiscent of a person on crutches: the pectoral fins (like crutches) bear the weight of the fish's body as it moves forward; only at the end of the stroke is weight transferred briefly to the pelvic fins. The other gait superficially resembles the walk of terrestrial vertebrates, which ambulate by moving alternate limbs. The pectoral fins provide power for walking, while the pelvic fins serve only to stabilize the fish. Frogfishes also swim, doing so by undulating their body as they move. In addition, they often jet propel themselves through the water, a feat the fishes accomplish by ingesting large amounts of water and then forcing it backward through gill openings.

Ultrafast feeding mechanisms, jet propulsion and aggressive mimetic devices by themselves are not unique to frogfishes; each adaptation can be found in a wide variety of other fish species. Yet in no other group are so many highly evolved and complex adaptations integrated into a single organism. It is not just the ability to lure prey or to change color or to clamber across the substrate that makes frogfishes so interesting. More important, perhaps, is that natural selection has favored the evolution of so many specializations within a single family of fishes. Understanding the specialized morphological and behavioral adaptations of these aggressive mimics is—without question—a challenge that will continue to occupy investigators for many years to come.



*GEOGRAPHICAL DISTRIBUTION of frogfishes is widespread in tropical and subtropical waters. They are most abundant in coastal waters of Indonesia, the Philippines and other island groups of the South Pacific. Few species occur either north or south of the region indicated in color on the map; most prefer areas where the average annual water-surface temperature is greater than 20 degrees Celsius.*

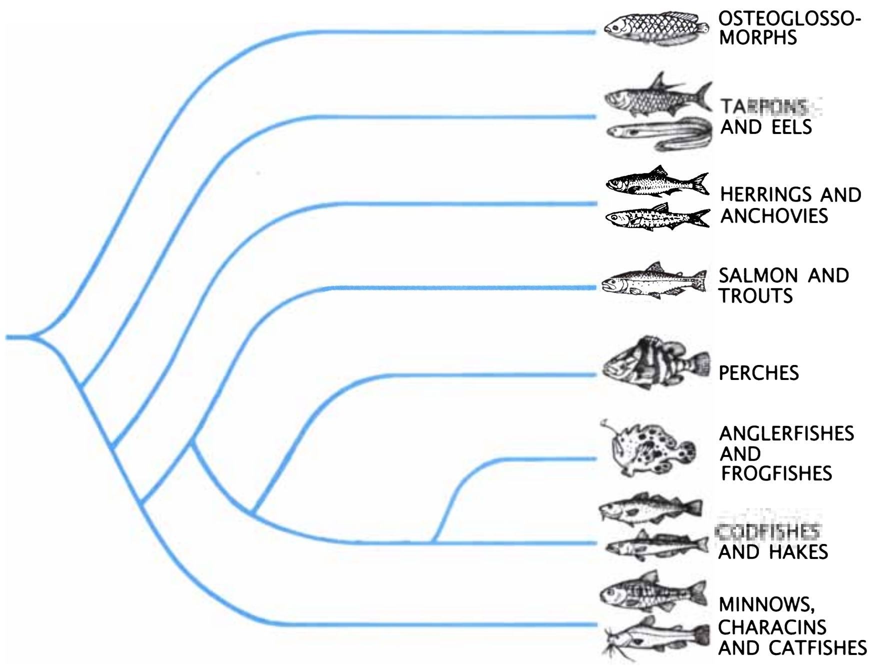



*DIAGRAM of the evolutionary relationships among bony fishes (the teleost fishes) indicates that anglerfishes are most closely related to codfishes and hakes.*


FURTHER READING

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