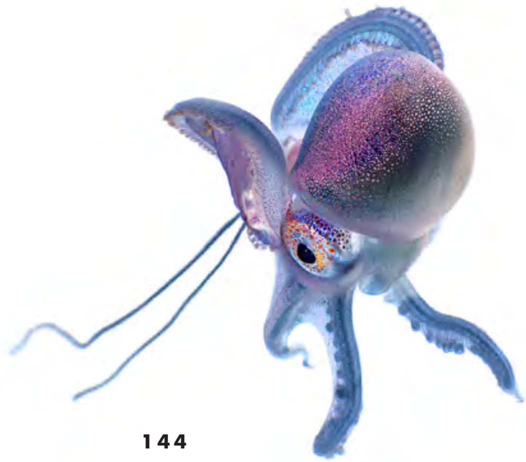

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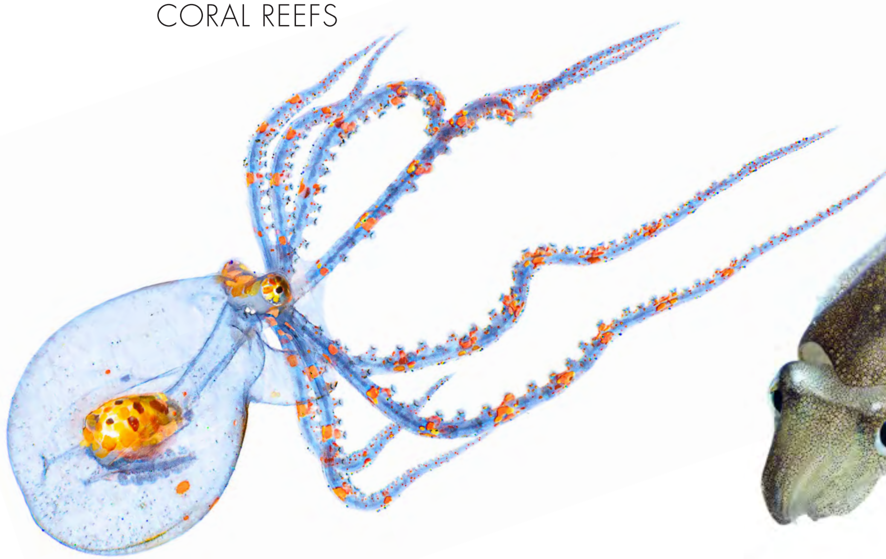
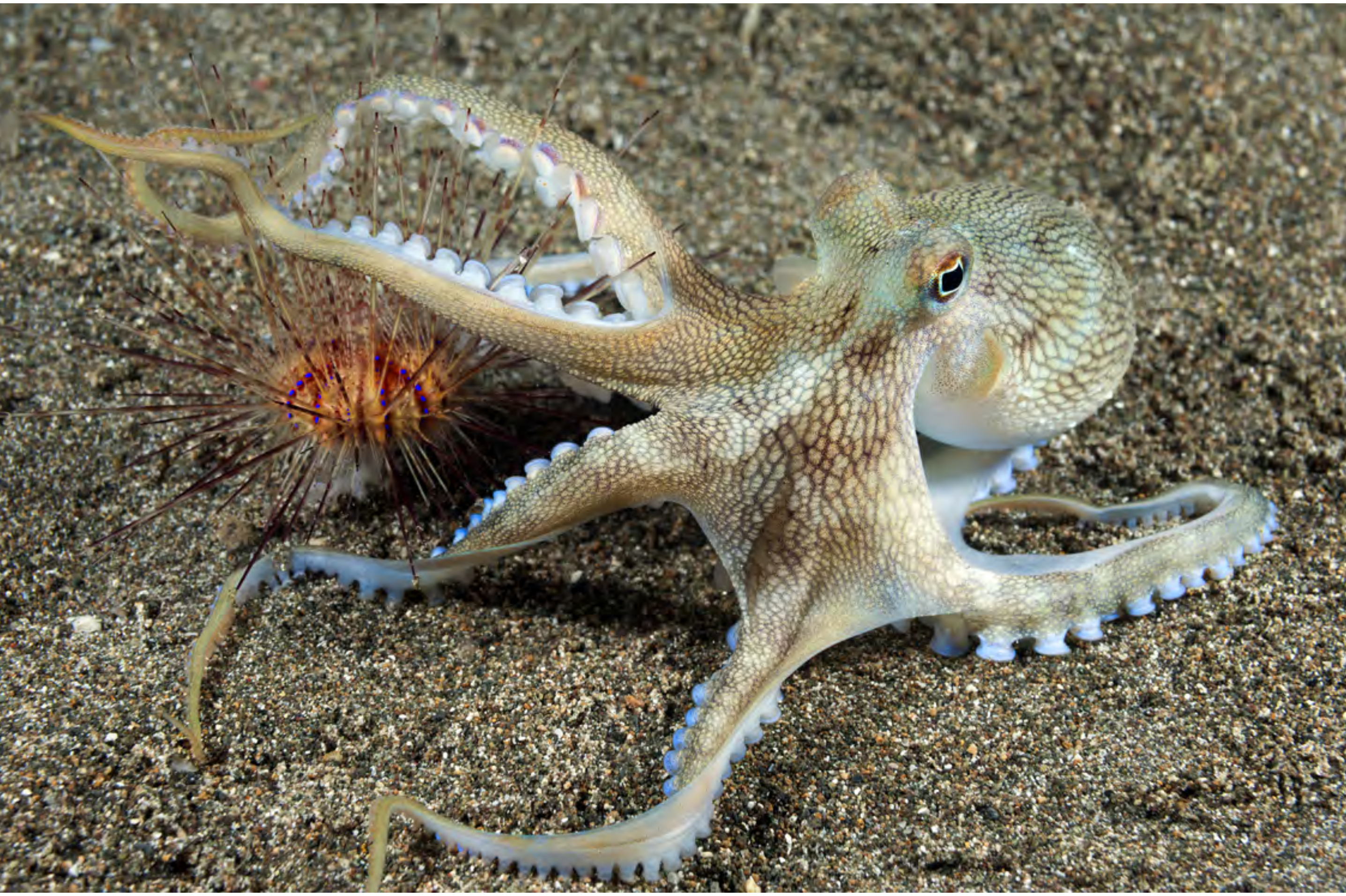


# Predator and prey

**Even the tiniest cephalopod paralarvae were thought to hunt for their food, until recent work on flying squid (Ommastrephidae) paralarvae revealed that they do not attack prey right after hatching. Instead, they scavenge bits of dead bodies, feces, and mucus. But they soon move on to capturing the tiniest possible prey: shrimplike plankton that feed on individual algal cells. As the squid grow, they integrate that planktonic nutrition into their bodies, building themselves big enough to go after larval fish and crabs, until eventually they can target adults of these same species.**



## HUNTING AND SCAVENGING TECHNIQUES

Cephalopods tend to be generalist predators, ready to attack whatever prey is available. In practice, any given environment tends to present a consistent array of prey species, so cephalopods can and do specialize. Some octopus species focus on drilling into snail shells and slurping out the contents; others munch primarily on crabs. Nautiluses, for their part, go after the cast-off molts of lobsters to get the calcium they need to build their own shells. And the Vampire Squid (*Vampyroteuthis infernalis*) collects detritus, similar to the dietary habits of flying squid paralarvae, but on a larger scale.

Cephalopods use their appendages to catch food: if tentacles are present, they can be shot out in a high-speed tentacular strike, almost like a frog's tongue going after a fly. Arms can capture food too, and if there are webs between those arms, they can engulf the prey in a deadly parachute. Appendages are sometimes considered part of a cephalopod's gape, the width of a predator's mouth. Gape size determines how big a prey item the predator can go after, and a cephalopod is not limited by the relatively small size of its beak. As long as it can keep the prey trapped in its arms, then it can take bite after bite until everything is consumed. What's more, some species have venom that can dissolve biological tissue, further breaking down large prey items.

## PREDATORS ON CEPHALOPODS

Over the course of their lives, cephalopods integrate energy and nutrients from a wide range of sources into a single delicious package that is, in turn, eaten by a huge range of predators—including humans. So far, we haven't managed to eat any cephalopod species to extinction. It would be nice to keep it that way, especially because squid are an integral part of so many other animals' diets: toothed whales, dolphins, porpoises; seals and sea lions and otters; seabirds, especially albatrosses; fish of many kinds, from sharks to rockfish to eels. All of these animals depend on an abundance of cephalopods throughout the world's seas. There's a reason that frozen squid is one of the most popular bait items.

Given the evolutionary flexibility of cephalopods, displayed over hundreds of millions of years of evolution, it's actually surprising that they're all carnivores. Why haven't any cephalopods evolved to eat seaweed? Why haven't they evolved to farm algae inside their bodies? Plenty of other "carnivorous" animals, such as sea anemones and sea slugs, have mastered that trick. It's a mystery we can hold onto as we explore all the diversity we do know about.

The rest of this book will be organized by habitat, so we can visit cephalopods in their own homes. We will explore the physical, chemical, and biological properties of each habitat before meeting the cephalopod species that reside there.

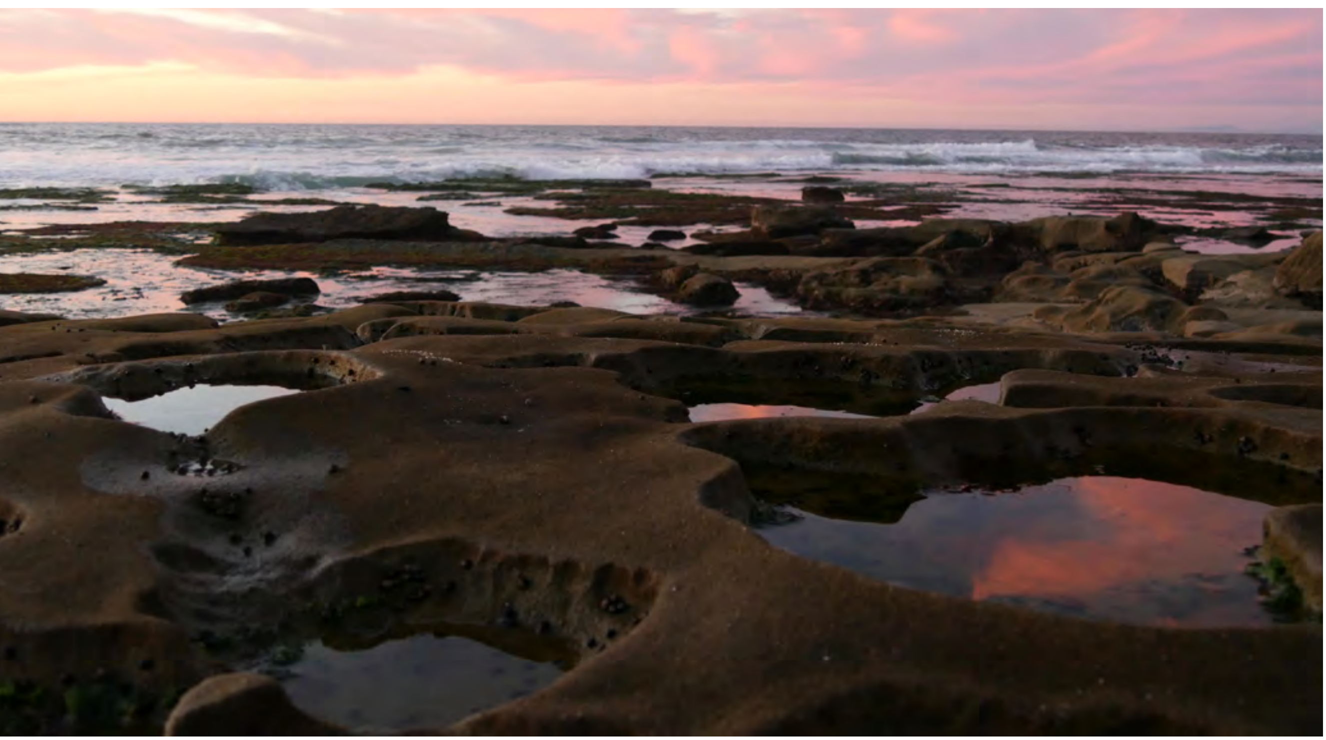
↗ Anemones, although sedentary, are voracious predators and scavengers. This small cephalopod may have been caught alive by the anemone's stinging tentacles or it may have been collected after dying from other causes.

← As exploratory hunters, cephalopods like this octopus may encounter new potential prey items, and learn through experience whether they are worth consuming.

# BEACHES, TIDE POOLS, SANDFLATS, & MUDFLATS

# At the interface of land and sea

**Some of the most striking human–cephalopod interactions occur when a cephalopod crawls out of the water, moving into our habitat seemingly to investigate us. One viral video in 2018 recorded an octopus at the Fitzgerald Marine Reserve in California oozing across seaweed-covered rocks, hauling the additional weight of a dead crab, which it deposited at the feet of the filming human before making its way back to the water. "What a friendly dude," the camera operator commented. Another viral video in 2021 recorded a more aggressive interaction on a beach in Western Australia, where an octopus struck a beachgoer several times with its arms, earning a reputation as the "angriest octopus" on the beach.**



## MOVING ONTO LAND

Do our anthropomorphic interpretations hold any water? Perhaps these octopuses were attracted to, or confused by, some stimulus we wouldn't even notice. Is there any way to determine the "real" motivations of cephalopods in these interactions, or can we only make imperfect guesses? What's certain is that very few ocean animals come onto land voluntarily. Seals and otters are exceptions, since they give birth on land, but truly marine mammals like whales and dolphins are in trouble if they get stranded on a beach. A few unusual fish can propel themselves out of water and survive for a time, and crabs can trot around on land and even, in the highly unusual case of the coconut crab, climb trees. However, the vast majority of marine life sticks to a habit of full submersion.

The space where sea meets land seems like it ought to be a barren expanse, where neither terrestrial nor marine life can thrive. However, this habitat has been around for longer than life has existed on Earth, and many groups of animals have evolved adaptations to inhabit this liminal space. Explore any rocky tide pool or sandy beach, and you'll find a range of barnacles and clams, crabs and anemones, worms and snails. And, if you're lucky, cephalopods.

Cephalopods tend to be some of the hardest tide pool inhabitants to spot, which might be why we get so excited when we do. One reason you're less likely to see a cephalopod than a snail is that cephalopods are relatively large predators, and any ecosystem can only sustain a limited number of those. Think of a forest, and how many more rabbits and deer it contains than wolves. Another reason we rarely see cephalopods on the beach is that they tend to be night-active, while humans tend to be day-active. And finally, of course, cephalopods have those remarkable camouflage abilities (see pages 30–33).

## OCTOPUSES AND HUMANS

Elusive as they are, however, the cephalopods at the interface of land and sea were the first cephalopods that we humans became acquainted with. These are the octopuses that found their way into ancient paintings and frescoes and onto pottery. People have discovered time and again that octopuses will happily climb into and inhabit human-created objects, from ceramic jugs to discarded cans and bottles. Fishing for octopuses by putting pots in the water and then hauling them back up is a long-standing tradition.

↗ Octopus vases are recognizable pottery from the Minoan civilization, which thrived on Crete and other Aegean islands 5,000 years ago.

← Many animals are adapted to life in these transient habitats, alternately connected to and disconnected from the rest of the sea.

← Although most species are nocturnal, octopuses can occasionally be spotted by daytime beachgoers.

→ The markings of a blue-ringed octopus can be hidden from view when it wants to camouflage, or be brought into bright emphasis to frighten away predators with the message: "I'm venomous, don't mess with me!"

### PLINY AND THE OCTOPUS

Humans must have been curious about cephalopods for as long as we've known about them. That's our scientific impulse: to ask, what are these creatures? How do they live? Why do they act the way they do? In one of the first European works of natural history, Pliny the Elder (23–79 CE) wrote about an octopus that not only crawled out of the sea, but made its way through a fence and into a factory to partake of the ancient Roman delicacy of fermented fish guts. According to Pliny, the octopus had an arm span of over 20 ft (6 m), which could have been true or could be an example of our human tendency toward exaggeration.

Of all cephalopods, octopuses predominate at the ocean edges because they are the crawlers; most squid and cuttlefish and all of the nautiluses are swimmers. Tide pools and beaches are not great places for swimming. However, we will meet a cuttlefish, and a couple of cuttlefish cousins, that have adapted to a bottom-sitting, rock-sticking lifestyle. Octopuses, though, have really spread into this habitat. Both the tiniest and the largest octopus species occur here, illustrating that this ecosystem, despite its narrow width, has a lot of niches to fill.

Our interaction with octopuses at the rim of our terrestrial home has typically been tinged with a hint of danger, to a variable extent depending on how large and how venomous the octopuses are in that particular part of the world. All octopuses have some amount of

venom in their saliva, but in most species it's not strong enough to seriously hurt humans. The exceptions are the blue-ringed octopuses (*Hapalochlaena* spp.) in the Indo-Pacific—and these do, in fact, inahbit the intertidal. They are not aggressive, however, and would much prefer to flash their bright colors and warn us away than to bite. Most cases of bites have occurred when human behavior was particularly reckless.

## WELCOME TO THE INTERTIDAL

The intertidal is an interesting place to do science. It's right there next to land—you don't have to get on a boat or in a submersible or send down a robot. And yet, it's a rough environment. Scientists and their equipment must struggle with all the same challenges as the organisms making their home there. Thus, despite their proximity to us, intertidal cephalopods have retained a great deal of mystery, and many of the species profiled in this chapter and their amazing habits were only very recently uncovered.

Let's metaphorically wet our feet with a foray into the intertidal zone—the part of the marine habitat that exists at the edge of the land. Some of us humans have lives tightly tied to the tides: fishers, oceanographers, those who live and work on coastlines. Others may have never seen a rising or falling tide. Many animals, though, depend on the tides for their very existence, because the changing height of the sea creates an entire complex ecosystem.

# Tides and their impacts

**Depending on where you live in the world, you might have more or less experience with tides. While very large bodies of fresh water have slight tides, an ocean is necessary for a significant tide and, even then, there's a lot of variation in tidal height from place to place. In the Bay of Fundy, Canada, the height of the sea can change 40 ft (12 m) from low to high tide. In Honolulu, Hawaii, the height rarely changes more than 1½ ft (0.5 m).**

↗ If you make a large wave in a swimming pool, it can travel to the other side in less than a minute. But a wave takes hours to cross the large Bay of Fundy—almost exactly as many hours as the span between low and hide tide. This natural resonance amplifies the tidal height.

## GRAVITATIONAL PULL

Tides are created by the gravitational pull of the moon, which, despite its seemingly mystical connection to the sea, actually pulls just the same on all of planet Earth: rock and soil and water alike. However, the solid parts of Earth are not easily deformed. The vast oceans, by contrast, can swell and slosh and sink.

Gravity gets stronger when masses get closer. So, the water on the side of Earth closest to the moon experiences the strongest gravitational pull, and bulges out toward the moon. Meanwhile, Earth itself is pulled slightly toward the moon, though not as much as the water closest to the moon. And the water on the far side of Earth, farthest from the moon, is also being pulled toward the moon—but less strongly than Earth itself is being pulled. So, this water on the far side also forms a bulge, since its total movement toward the moon is less than the total movement of Earth toward the moon. These two bulges of water on opposite sides of Earth are the high tides. They always remain in the same orientation relative to the moon, but since Earth itself is spinning, different parts of our planet rotate through and experience each day's two high (and two low) tides.

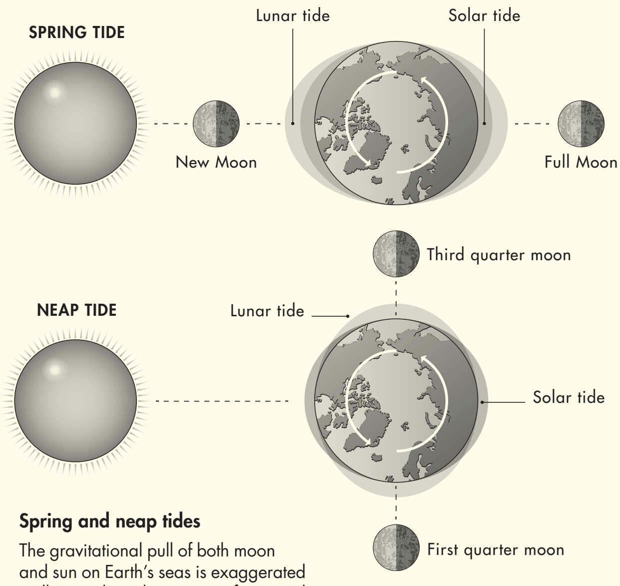
## TIDAL VARIATION

If that were all there were to it, tides would be the same all over Earth. But the planet is not covered with a single uniform ocean. It is covered with irregular ocean basins, hemmed in by asymmetrical continental shapes. The seas are constrained by both gravity and the physical limits of their space on the planet. When a lot of water is squeezed

into a smaller area, the tidal range (change in sea level from high to low tide) is greater. When the water has more room to move and circulate, the tidal range is less.

To add to the complexity, tides do not occur at the same time every day, but shift by about 50 minutes. This shift is caused by the "lunar day" being longer than the "solar day," because Earth keeps spinning as the moon travels around it, and the moon is always falling behind.

The height of the tide changes over the course of the year, as well. That's because the sun also exerts a gravitational force on Earth and its water. It's not nearly as strong as the gravitational force of the moon, because the sun is so much farther away, but it does play a role. When sun and moon are in alignment, both pulling in the same direction, we experience spring tides—the highest and lowest tides of the year. When they are working at odds, the moon pulling in one direction and the sun at a 90-degree angle, we experience neap tides—the most unremarkable, middling tides of the year.




**Spring and neap tides**
The gravitational pull of both moon and sun on Earth's seas is exaggerated to illustrate how they can reinforce each other to produce the twice-monthly spring tides, or work in opposition to produce the twice-monthly neap tides.

## INTERTIDAL HABITATS

Every space on the coast between the highest high-water mark and the lowest low-water mark, is considered the intertidal. The animals that live here have evolved to cope with an existence that not only encompasses land and water, but also contains some of the fiercest physical forces anywhere on the planet: regular, daily, pounding waves, and often extreme heat as well. If you've ever touched the water in a high tide pool on a sunny day, you may have noticed that it can reach bathtub temperatures.

Within the intertidal zone, each species has adapted to its own niche. Some intertidal creatures thrive at the highest limits, where they are almost never submerged and get all their moisture from the splash of waves and spray. Others can only survive in the lowest regions, where they are nearly always wet and their daily heat exposure is minimal. Still others can wander up and down.

↖ Mangrove forests are created by remarkable trees that have adapted to live in saltwater. The complex root architecture of these plants keeps them stable as tides rise and fall, and creates an important habitat for many animals.

↑ Where glaciers and ice shelves meet the sea, the intertidal habitat is dominated by ice. These areas look barren compared to other ecosystems, but many kinds of ice algae and microbes thrive here.

↗ This American Oystercatcher has ventured beyond the limits of its name to catch a different mollusk: an octopus. Shore birds are one of many risks faced by intertidal cephalopods.

Intertidal habitats can be rocky, sandy, muddy, or a mixture. They can be dominated by algae or seagrass, although these plants (or "plantlike things," as algae is technically not a plant) cannot live too long exposed, and are more abundant further down toward the sea. Many intertidal animals burrow into the sand and rocks, which offer protection from heat, desiccation, and waves. Others, such as snails and mussels and barnacles, make hard homes they can seal shut when exposed and open up when submerged.

The intertidal is an area in constant flux, as waves erode rocks and carry sand. Organisms themselves create and build the habitat, from worms that dig holes in rock to mussels that grow expansive beds, making spaces for small worms and crabs—and, of course, octopuses—to hide and crawl and hunt in.

Intertidal zones can be as steep as a cliff face, or as smooth as a sandflat or a mudflat. These "flats" are especially mutable habitats, as a rising tide can cover a huge area with quite shallow water, and a retreating tide can leave it dry again. Usually, if you dig down at all, you can find a bit of water. These areas act as "sponges" that hold significant amounts of liquid even when they appear dry on the surface. This allows burrowing animals to stay wet through the change of tides.

Cephalopods can't cement themselves down like a barnacle, or grow a hard protection like a snail's shell. But they have their own transient and flexible approaches to the challenges of the intertidal, from borrowing the protection of other animals to building dens and burrows for themselves in rocks, sand, and mud.

# Life in air and water

**Generally speaking, camouflage works great as long as you are very still. But if you're a cephalopod, you can't stay still forever—you have to move to hunt for your food. This is where the turbulent intertidal environment comes in very handy for cephalopods. They can camouflage themselves to blend in with other moving things, because the sloshing, crashing waves make everything move.**

## ADAPTATIONS TO LIVE OUT OF WATER

Breaking waves create a "splash zone" that gets hit by spray even higher than the high tide line. This can dampen animals that would otherwise be at greater risk of drying out. However, a little periodic splashing isn't enough to keep most cephalopods happy. They face a problem that their mussel and snail cousins do not. When out of water, shelled mollusks can clam up (forgive the pun). They seal their soft, wet parts inside a mostly impermeable shell, and lose little moisture to the air. Coleoids, having given up their protective shell, cannot do this. Yet it is coleoids and not nautiluses that have colonized the intertidal. A nautilus would be useless out of water, as its arms are not muscular enough to carry its body weight on land.

↗ Unlike squid, octopuses cannot swim far with jet propulsion. The pressure it produces inside their mantles actually stops their hearts!

← Although octopuses fall far behind squid when it comes to swimming underwater, their ability to move on land is unparalleled among their squid and cuttlefish cousins.

↙ This fossil of a Jurassic belemnite illustrates how sturdy this group's internal shell used to be. But with their skin on the ouside, these animals would have faced the same challenges to life in both air and fresh water.

The large surface area of exposed coleoid skin has several disadvantages. One is dehydration, losing water across the permeable membrane through evaporation. Another aspect of the skin's permeability may explain the absence of any freshwater cephalopods. Cephalopod internal fluids, like those of all animals, have a salinity not too different from that of the ocean. Animals that evolved to live in fresh water have adaptations to maintain their internal salinity above that of their environment. Otherwise, simple chemistry dictates that fresh water would continuously diffuse into their cells as the molecules seek an equilibrium. Cephalopods have never adapted to this situation.

The permeability of cephalopod skin also brings an advantage: it can be used to breathe. Gas exchange can occur across any thin membrane, not only in lungs and gills, and many invertebrates rely on gas exchange across their skin to provide them with enough oxygen. This "cutaneous respiration" likely plays a role in cephalopods venturing out of water, although the extent of its contribution remains to be studied.

Of course, cephalopods do have gills, like fish and crabs and so many other marine creatures. When animals with gills or lungs breathe, their aim is to bring oxygen into their bodies; specifically, into their bloodstreams. Both gills and lungs have evolved a large surface area to maximize the efficiency of transfer. Blood is passed over the inside of the surface, and air or water is passed over the outside, and oxygen-carrying molecules inside the blood bind the oxygen that diffuses across the membrane.

Zooming in on our lungs, you'd see that they are full of many tiny branching passages. Gills have a similarly large surface area, with lots of folded membranes to pass water over. However, when gills come out of the water, these folds stick together, drastically reducing their surface area and making them almost useless for pulling oxygen out of the air. Even though a cephalopod's gills are protected within its mantle cavity, the mantle is likely to deflate out of water, leaving the gills and other internal organs all pressed together until the animal can refill its mantle and fluff up its gills.

However, as long as the animal returns to water before it dries out or suffocates, there are no ill effects of such "deflation." And here's another difference between cephalopods and vertebrates: our oxygen-binding proteins. Vertebrates have hemoglobin, which uses iron to bind oxygen. That's why it turns red (rust-red) when oxidized. Cephalopods have hemocyanin, which uses copper to bind oxygen, and it gives their blood a distinctive blue-green color. Hemocyanin isn't as good at binding oxygen as hemoglobin, which limits cephalopod activity in some situations, but in the case of crawling around on land, it may expand the time it takes them to use up the available oxygen by slowing down the process of binding and releasing this crucial compound.

## WAVE ACTION

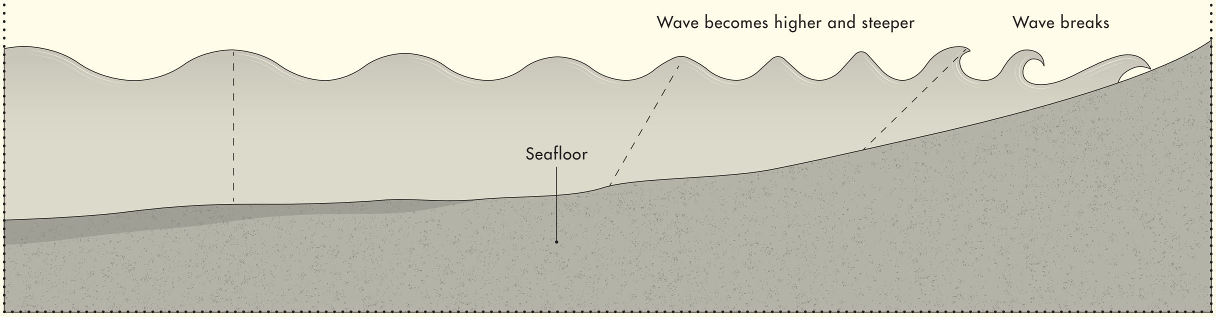
The intertidal area exists because of the tides. However, at any given moment, there's usually a far more noticeable force at work: wave action. Waves, whether huge breakers that surfers dream of or tiny ripples lapping at your feet, are not caused by the gravity of the moon or the sun. They are instead the product of physical agitation of the water, usually by wind, but occasionally by disturbances such as whales and boats.

You may have heard the term "tidal wave," and wonder where that fits into the tide/wave distinction. Because of this understandable confusion, "tidal wave" is falling out of use in favor of more specific terminology. When the rising or falling tide causes a visible rush of water, because it's being funneled through a narrow opening, that's a tidal bore. By contrast, a tsunami occurs when a huge amount of water is shifted—often by seismic activity, such as an earthquake or a volcano. Finally, a storm surge is a large rise in water level driven by meteorological activity.

All these water movements can contribute to the extreme conditions already present in the intertidal zone. However, they are sporadic, while regular wave action driven by wind is a continuous assault, minute by hour by day. The size of these ordinary waves is determined by two things: the fetch, or distance over which the wind has been blowing, and the angle of the shore onto which the wave is moving. As a wave moves from the open sea toward the shallower shore, its bottom drags on the ground and is slowed down, while the wind keeps pushing on its top. Eventually, this push–pull causes the top of the wave to "break."

**Breaking waves**

Waves are traveling patterns, not traveling water. As the pattern moves from deep to shallow water, the bottom of the wave is slowed by the seafloor and the top falls foward, like you might fall forward if your feet were slowed down by tripping on something.



### TERRESTRIAL PREDATORS

In addition to death by asphyxiation and dehydration, another intertidal danger is the risk of terrestrial predators—from bears and wolves to humans. All around the world, people venture into tide pools and onto sand- and mudflats to harvest seafood. Experienced fishers know how to identify an octopus den, even when to the untrained eye it looks exactly like the surrounding rocks and coral rubble. They need no sophisticated technology, not even any bait—just a sharp stick and a fast hand.

↓ A fisherman of the Dumagat people in the Philippines collects octopuses alongside other marine species. Without bones or scales, cephalopods can be an easily prepared protein for many people.

# Burying and burrowing

**All that wave action we've discussed leads to a lot of erosion, which is one reason we have beaches. Sand is made of tiny bits of rock broken off and worn down by year after year of pounding waves, along with pieces of shells and bones ground down in the same way.**

## BEACH ADAPTATIONS

Another reason for beaches is the carrying of sediment by rivers and streams. Fresh water tends to flow quickly down mountains, slowing down as it moves along less steep inclines out to the sea. Fast water can bring mud and sand and even rocks along, while slow water drops these passengers to the riverbed. Many rivers open up into deltas when they reach the coast, and this is where the sediment they've been carrying settles down.

What does this have to do with cephalopods? Well, changing your colors to match your environment works best when you have a colorful environment. In a home full of different corals and rocks, encrusted with a profusion of animals and algae, the cephalopods' ability to change their skin color and texture shines. However, on the wide expanses of sand and mud that characterize a great deal of the land–sea interface, this talent may come in less handy. Here on the flats, some spectacularly specific adaptations have evolved to cope

→ This Coconut Octopus is engaged in a combination of hiding and burying. It clings with its suckers to the inside of an empty clam shell, which is itself partially buried in the gravel and detritus of the seafloor.

← Getting sand in the eyes is an unpleasant beach experience for humans, but cephalopods that dig and burrow in sand have a transparent covering to protect their eyes.

with an environment that is physically monotonous, but temporally highly variable. Two distinct adaptations are burying and burrowing. There are many other animals that bury and burrow, but as in nearly everything else, cephalopods do it in their own ways.

## DIGGING TECHNIQUES

Burying animals include humans, and you may even have participated in such activities on childhood trips to the beach. All you have to do is lie down, maybe wiggle yourself into a bit of a depression, and use hands or shovels to cover yourself with sand. Sand-dwelling octopuses and bobtail or bottletail squids will typically use a jet of water to clear a depression in the sand or mud, then settle down and use two of their arms to scoop and sweep sediment up over their bodies.

Burrowing takes more effort. You can only claim to have burrowed into the sediment if you've dug a hole deep enough to get yourself entirely below surface level. Plenty of animals do this: many different kinds of worms, clams of all sizes up to the giant geoduck, and the little sand crabs or mole crabs that many beachgoers enjoy digging up from the surf zone. However, it was only in 2015 that an octopus was discovered to be capable of such a feat (see page 66).

Covering oneself with sediment might seem to obviate any need for camouflage, but these cephalopods are usually very capable of also matching their skin to their hiding place. After all, they need to leave at least a little bit of themselves exposed to keep breathing.

# How and why cephalopods make their own glue

**A covering of sand sounds like temporary concealment at best, in an environment full of splashing and crashing waves. The cephalopod solution is mucus. As humans, we think of it as an unpleasant substance in our noses. In truth, mucus is formed and used hroughout our bodies, and we couldn't live without it. But as important as mucus is to humans, it's even more important to mollusks.**

## MOLLUSCAN MUCUS

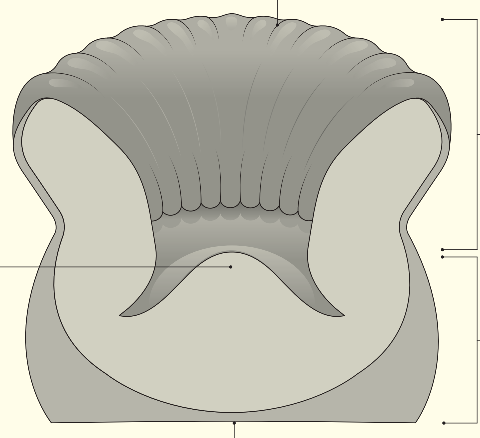
Snails and slugs on land leave mucus trails that may be familiar from gardens and sidewalks. The trail is not the point, though, it's merely a side effect of the self-lubricating foot that these mollusks use to move around.

You might think that aquatic mollusks, being in the water, wouldn't need as much mucus. In fact, they have even more uses for it. Mucus can interact with water for a huge range of applications. Thick mucus can entangle and deter predators. Mucus nets or bubbles can be used to capture food. Thin, slippery mucus can be secreted to protect the skin and wash off debris. Mucus can be mixed with pigments to create a smokescreen of ink, a habit of both cephalopods and some of their sea slug relatives. Mucus can even be a home for beneficial microbes, such as bacteria that share nutrients with their host or produce antipredator defense chemicals. This kind of

← Octopus sucker cups range from microscopic to the size of a child's hand. They regularly shed and replace their outermost layer.

**Getting a grip**

Tiny grooves lining the infundibulum help sucker cups grip wet, irregular surfaces. Scientists have also found that the tissue of the infundibulum is extremely soft and malleable, allowing it to mold to match the shape of whatever the octopus might cling to.




interaction, with two or more organisms providing mutual aid, is a mutualism—the most well-known type of symbiosis. (Symbiosis, which simply means "living together," also includes antagonistic interactions such as parasitism. Scientists are discovering the fluidity of the distinctions between mutualism, parasitism, and commensalism, or neutral cohabitation. Environmental changes can shift a relationship from one kind to another.) And mucus can be glue.

## SUCTION POWER

Cephalopods are already well known for having their own special way of sticking onto things: suction cups. Their arms are lined with hundreds of suckers, from large ones as big as a human child's hand at the thickest part of the arm of a giant octopus, all the way to nearly microscopic suckers at the slender arm tips. They create suction mechanically, by forming a seal around the rim to prevent water from entering the cavity inside the sucker, then pulling against that cavity to create a region of low pressure. This works excellently on smooth glasl, as many people have observed. However, the intertidal environment doesn't contain much smooth glass. What it does have is a lot of irregularly shaped rocks and shells and algae, with grit scattered over them.

In 2013, scientists took a closer look at octopus suckers, and found that they have a microstructural adaptation to deal with this: very small and very regular grooves along both the rim and the center of the sucker cup. The material of the sucker rim is also very soft, and this combination of roughness and softness creates a surface that can seal against nearly any other surface. One of the few substances that a cephalopod sucker will not stick to is the cephalopod itself. This fascinated the researchers who noticed it—how does a sucker recognize "self"? The answer appears to be a kind of taste. Octopus arms secrete distinctive chemicals, and their suckers contain sensory receptors that can recognize these chemicals and decide not to attach.

## CEPHALOPOD GLUE

Possibly because suckers themselves are so obvious and interesting, it's taken scientists a while to study the adhesive potential of cephalopod mucus in more detail. We're just starting to get a handle on how prevalent its use is. Research published in 2007 listed only four cephalopod genera known to produce adhesive mucus; more are likely to be discovered.

Given their affinity as mollusks, cephalopods have probably been making slimes of various kinds since they first evolved. This is further supported by the fact that one of the known glue-making genera, *Nautilus*, diverged from all the others hundreds of millions of years ago. Nautiluses do not have mechanical suckers on their tentacles, and instead use mucus to make their tentacles sticky. By secreting special slime from cells in their tentacles, they can stick to prey and mates and cling to their environment as needed.

Coleoid cephalopods don't seem to make mucus with their arms; instead, they secrete it from special glands in their mantles. Several intertidal cuttlefish glue themselves down to hard substrates, such as rocks or human-created surfaces, likely to resist being buffeted by waves. The limited studies that have been done so far suggest that they use a combination of mechanical and chemical adhesion, both producing sticky slime proteins and physically contracting the center of their mantle to create a giant sucker cup.

Bobtail squids, by contrast, secrete their sticky glue all over the top of their mantles. They combine slime with burial, whisking sand over their bodies and gluing it in place for camouflage. They can release this coat of mucus plus sediment instantly, if necessary for escape. Pygmy squids (*Idiosepius* spp.) also have glue glands on the top of their mantles, though in a more specific spot close to the fins. Instead of attaching sand to themselves, they use this glue to attach themselves to the underside of seagrasses, where they sit and wait for prey to come to them. Like the bobtail squids, they can release the attachment instantly.

In both cases, the animals have two different kinds of slime-making cells. A two-part slime system can work in one of two ways. In bobtail squids, the quick release seems to be made possible by a "duo-gland" system, which creates one kind of chemical that does the sticking, and a different kind that does the unsticking. However, in pygmy squids, the two kinds of cells produce two substances that mix together to make the glue, more like a two-part epoxy. The release, then, is accomplished not by producing a third chemical, but by physically breaking the seal with the substrate.

Not all cephalopod slime turns out to be true mucus. A particular set of proteins called mucins is necessary to merit that designation, and recent protein characterization of bottletail squid slime turned up no mucins at all. It would appear that cephalopods have evolved a variety of original ways to slime it up, and we're just beginning to figure out what those chemicals are, and how they work.

← Pygmy squids are just one of many varieties of organisms that benefit from attaching themselves to seagrass. Bryozoans (also known as moss animals), hydroids (relatives of anemones), and an array of algae are some of their common companions in this habitat.

ABDOPUS ACULEATUS

# Algae Octopus

Seaweed mimic

| | |
|---|---|
| SCIENTIFIC NAME | *Abdopus aculeatus* |
| FAMILY | Octopodidae |
| MANTLE LENGTH | 2¾ in (7 cm) |
| TOTAL LENGTH | 10 in (25 cm) |
| NOTABLE ANATOMY | Algal camouflage |
| MEMORABLE BEHAVIOR | Bipedal locomotion, "land octopus" |

**Memorably described by David Attenborough in a BBC Earth documentary as "the only land octopus," the Algae Octopus is certainly the cephalopod species that is most comfortable on land. It still requires seawater to live, so it's not exactly terrestrial, but it routinely crawls from pool to pool, hunting for food.**

Underwater, its movement is also remarkable. Along with the Coconut Octopus (*Amphioctopus marginatus*, see pages 64–65), the Algae Octopus was one of the first two octopus species to be observed by scientists engaging in bipedal locomotion—walking on two limbs. We humans are somewhat understandably obsessed with other animals' behavior when it reminds us of our own, so this discovery made news headlines.

Apart from its humanoid appearance, bipedal walking intrigues us with the opportunity to compare its mechanisms between species. Prior to its discovery in these octopuses, the majority of known bipedal locomotion occurred in vertebrates—primates, birds, the occasional lizard. Our bones, joints, and muscles work together to create a balanced gait. How could invertebrates, with no bones and no joints, accomplish something similar? The only one observed to do it occasionally had been the cockroach, which still has a tough jointed external skeleton.

Researcher Christine Huffard described octopus walking evocatively: "The octopus rolls along the sand as if on alternating conveyor belts." Without joints, there is no real distinction between "foot" and "leg." The end of one arm is simply laid down on the sand, then pushes off from imaginary "heel" to "toe" in a single continuous movement, while the second arm is laid down in advance of the first, preparing to repeat the pushing-off movement. The octopus's stride length is thus far less constrained than our own, perfectly embodying the quote often attributed to Abraham Lincoln that a man's legs should be "long enough to reach from his body to the ground."

The Algae Octopus does not walk on two arms in order to look like a human, but it is mimicking something else—a drifting clump of algae, as you might guess based on the species name. Wrinkling and ruffling its skin, it spreads and curls its other six arms around its body to resemble a cluster of seaweed. The two walking arms could be no more than pieces of loose algae, trailing along the bottom as the current carries the "definitely-not-an-octopus" along.

→ The scientists who first observed walking Algae Octopuses had to laugh at the visual absurdity of their gait—but they also had to analyze and appreciate the complexity of a behavior that has clearly served this species well when it comes to survival.

**AMPHIOCTOPUS MARGINATUS**

# Coconut Octopus

Mobile homeowner

| | |
|---|---|
| SCIENTIFIC NAME | *Amphioctopus marginatus* |
| FAMILY | Octopodidae |
| MANTLE LENGTH | 3¼ in (8 cm) |
| TOTAL LENGTH | 6 in (15 cm) |
| NOTABLE ANATOMY | Typical color pattern of dark branching "veins" |
| MEMORABLE BEHAVIOR | Bipedal locomotion and tool use |

**For an octopus, this species has attained a level of fame few others can aspire to. Once known simply as the Veined Octopus for its resting color pattern, it has made headlines twice already in the twenty-first century: in 2005 for its ability to walk along the sandy seafloor using only two arms, a form of bipedalism, and in 2009 for its habit of carrying around coconut halves as a mobile shelter, an activity that constitutes tool use.**

Both behaviors likely evolved in response to the octopus's habitat in the tropical western Pacific, where it lives in very shallow water close to shore. Although coconut trees do not grow in the sea, the octopus lives in a habitat so close to coconut-filled islands and coasts that its sandy seafloor habitat is full of coconut shells. Waves and currents often push these shells along the sand. When the octopuses gather six of their eight arms around their head and mantle, leaving two arms free to push off the bottom, they look not unlike a bobbing coconut. To be sure, coconuts do not walk on two legs, but neither do octopuses as a general rule, so the animal confuses its predators either way.

For their second astonishing behavior, Coconut Octopuses stack two coconut halves like bowls, then carry the stack under their arms and walk along with their arms around the outside of the shells. This isn't bipedal, but it is weird enough to get its own name, "stilt-walking," and scientists point out that it's pretty inefficient. Stilt-walking is only useful because it lets them carry protection, which they then have to stop and assemble, flipping one of the halves over to create a spherical lair.

This was considered the first evidence of tool use in an invertebrate species, where a "tool" is an object that "provides no benefit until it is used for a specific purpose." If octopuses merely hid in coconut shells when they came across them, as they hide under rocks and inside snail or clam shells, that would not really be tool use. The key innovation here is that the octopuses actually carry the coconut shells around with them, at some cost to themselves, anticipating a future use.

→ Humans use different parts of the coconut plant for food, fibers, and fuel, in cosmetics and as building materials. The usefulness of coconuts extends even beyond all that humans do with them. Resourceful Coconut Octopuses have learned to utilize the empty shells as mobile homes.

OCTOPUS KAURNA

# Sand Octopus

Subterranean slimer

| | |
|---|---|
| SCIENTIFIC NAME | *Octopus kaurna* |
| FAMILY | Octopodidae |
| MANTLE LENGTH | 3⅓ in (8.5 cm) |
| TOTAL LENGTH | 16½ in (42 cm) |
| NOTABLE ANATOMY | Very long arms |
| MEMORABLE BEHAVIOR | Subsurface burrowing |

**Named after the Aboriginal Kaurna people of South Australia, this octopus is distinctive in both physical appearance and habits. Its arms are extraordinarily long, and it is the only known octopus to truly burrow beneath the surface of its sandy habitat.**

Although such burrowing had been suspected previously, it was first examined and studied in scientific detail in 2015. Researchers observed Sand Octopuses burrowing in the wild as well as in the laboratory, where they built aquariums in the shape of scaled-up ant farms so they could watch the process of burrow formation through clear glass.

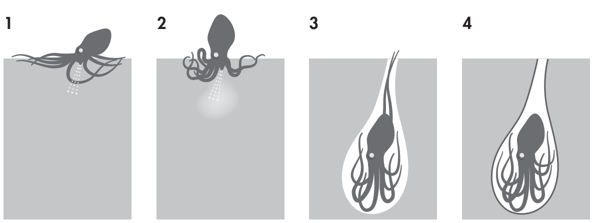
Sand Octopuses make their burrows not by digging with their arms, but by blasting water from their siphon. These jets of water "fluidize" the sediment, in the same way that shaking a jar containing both sand and water temporarily suspends the sand particles in the water. The octopus can move right into the fluidized sediment, just like you can swim through a muddy lake even though you can't swim through mud that has settled to the bottom of the lake. The octopus first enters with its arms, keeping both mantle and funnel above the surface to suck in water and blast the burrow bigger, until there's enough fluidized sediment to fit its whole body below ground.

So far so good, but the sediment won't stay fluidized. How does the Sand Octopus keep from suffocating once it's well and truly buried? Before the sediment completely settles down, the octopus reaches two arms up to the surface to make the shape of a chimney, like a snorkel for breathing. Then it uses slime to solidify the walls of both chimney and burrow.

Cephalopods are masters of repurposing the efforts of other animals, happily occupying empty snail and clam shells. Sand Octopuses are no exception, and have been seen occupying worm burrows to save themselves the trouble of fluidizing their own sediment. Scientists don't know yet how the Sand Octopuses produce the slime, what the slime is made of, or how it's integrated into the sediment.

**How the Sand Octopus burrows**

1. Fluidizes sediment with a water jet
2. Slides in arms first. Repeats steps 1 and 2 until buried
3. Uses arms to shape a chimney
4. Cements burrow walls with mucus




→ The Sand Octopus's habit of digging a sand burrow and securing the walls with slime is reminiscent of the garden eel, which also lives in tropical sandy habitats and makes a mucus burrow —a good example of convergent evolution in fish and cephalopods.

MACROTRITOPUS DEFILIPPI

# Atlantic Longarm Octopus

Flatfish impersonator

| | |
|---|---|
| SCIENTIFIC NAME | *Macrotritopus defilippi* |
| FAMILY | Octopodidae |
| MANTLE LENGTH | 3½ in (9 cm) |
| TOTAL LENGTH | 12 in (30 cm) |
| NOTABLE ANATOMY | Very long arms, distinctive paralarva |
| MEMORABLE BEHAVIOR | Flatfish mimicry |

**This tricky octopus existed for many years in the minds of scientists as two separate species: *Octopus defilippi* and *Macrotritopus equivocus.* The former was an adult octopus that roamed shallow sandy habitats, eating crabs and burying itself in the sediment. The latter was a transparent octopus paralarva that drifted in the plankton, two of its eight arms far longer than the rest.**

Eventually, scientists raised *Macrotritopus equivocus* paralarvae to adulthood and found that they metamorphosed into *Octopus defilippi*. A few years later, the connection was confirmed when adult *O. defilippi* laid eggs in captivity, which hatched into *M. equivocus* paralarvae. The two names were merged, with *Macrotritopus* becoming the new genus. (Octopus researchers tend to be eager to place *Octopus* species into new genera. For a long time, the genus *Octopus* was vastly overused as a "wastebasket taxon," a group into which every new species that didn't obviously belong anywhere else was dumped. Scientists are still clarifying the distinctive features of the genus *Octopus*, and which species don't belong there.)

Like both Algae Octopus and Coconut Octopus, the Atlantic Longarm Octopus needs to move across its shallow sandy habitat and, also like them, it prefers to look like something else when it does. It arranges its arms and mantle into a wide, flat ovoid, with the trailing tips of the arms resembling the tail of a flatfish. This flatfish mimicry was even observed in a paralarva that was reared to adulthood in captivity, although the octopus had never in its life encountered a real flounder. This suggests that the behavior is a stereotyped evolutionary adaptation, hardwired into the genome, rather than something that is learned by exposure.

One has to wonder about the advantage. Flatfish are not poisonous, so the Atlantic Longarm Octopus cannot take advantage of local predators' avoidance of known poisonous species. Flatfish are, however, full of bones, which makes them somewhat more challenging to eat than the boneless "protein bar" of an octopus. All other things being equal, there's not much better food than an octopus for a marine predator, so for an octopus to resemble almost anything else is probably a reduction in the amount of unwelcome attention it receives.

→ The unusually long arms of *Macrotritopus defilippi* give this species a lot of material to mold into shape for its characteristic flatfish mimicry.

WUNDERPUS PHOTOGENICUS

# Wunderpus

Delicate beauty

| | |
|---|---|
| SCIENTIFIC NAME | *Wunderpus photogenicus* |
| FAMILY | Octopodidae |
| MANTLE LENGTH | 1¼ in (3 cm) |
| TOTAL LENGTH | 8 in (20 cm) |
| NOTABLE ANATOMY | Dramatic fixed markings |
| MEMORABLE BEHAVIOR | Mimicry of venomous animals |

**This species was referred to as the Wunderpus before it even had a scientific name, due to its incredibly dramatic—and, unusual among cephalopods, fixed—coloration. The high-contrast brown and white bands on its arms and the splotches on its mantle are very similar to those displayed at times by the closely related Mimic Octopus (*Thaumoctopus mimicus*), but the Mimic Octopus readily changes its patterns. The Wunderpus does not.**

Because it stands out so noticeably against its sandy habitat, and because it lives in shallow water relatively easy to access by recreational divers, the Wunderpus also accumulated quite a collection of celebrity photos by the time researchers gave it a scientific name. Hence the species: *photogenicus*.

If we humans can see it so well, it stands to reason that other visual predators can also spot the Wunderpus. In fact, that may be the adaptive value of the pattern. Although this species does not imitate as many other species as its cousin the Mimic Octopus, Wunderpus octopuses are known to mimic two other species with which they share their conspicuous banding pattern: the lionfish and the sea krait (a kind of sea snake). Both are extremely venomous, the lionfish injecting toxins through its spines and the sea krait through its fangs. Thus, the Wunderpus may be using a strategy called Batesian mimicry, making predators think it is dangerous simply because it resembles another dangerous animal.

Because of its beauty, both professional and hobby aquarists have attempted to keep Wunderpuses. However, these octopuses do not adapt well to captivity, losing their coloration and remaining hidden as much as possible. Even more problematic is the fact that they live only in the tropical Indo-Pacific, and we don't know how large their populations are. Collecting tropical animals for the aquarium trade always means collecting more than will be sold, because long-distance shipping is stressful and not all will survive. Any demand for these animals in captivity could be dangerous to their survival in the wild. It's much better to enjoy them in their natural habitat, either in person if you live close enough (or can travel), or by appreciating the gorgeous photos and videos made available by local divers.

→ The Wunderpus defies the octopus stereotype of hiding in plain sight by attracting attention with its bold markings—like the brightly colored butterflies on land that warn away predators with their patterns.



(continued...)

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