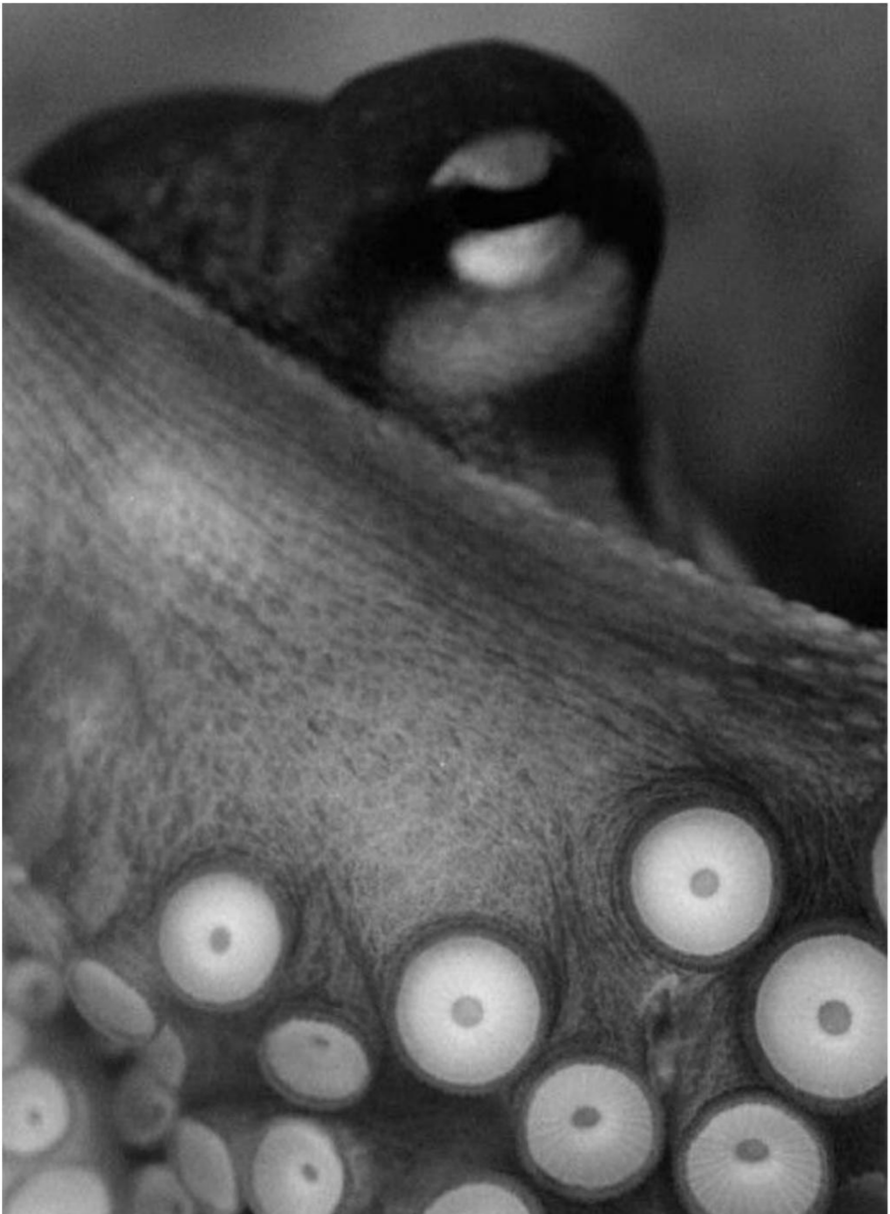


Published in 2010 by Timber Press, Inc.

The Haseltine Building
133 S.W. Second Avenue, Suite 450
Portland, Oregon 97204-3527
timberpress.com

2 The Quadrant
135 Salusbury Road
London NW6 6RJ
timberpress.co.uk

Second printing 2011
Printed in China

Library of Congress Cataloging-in-Publication Data

Mather, Jennifer A.
Octopus : the ocean's intelligent invertebrate / Jennifer A. Mather, Roland C. Anderson, and James B. Wood. — 1st ed.
p. cm.
Includes bibliographical references and index.
ISBN 978-1-60469-067-5
1. Octopuses. I. Anderson, Roland C. II. Wood, James B. III. Title.
QL430.3.O2M38 2010
594'.56—dc22

2009041311

A catalog record for this book is also available from the British Library.

Contents

Preface

Octopuses are intriguing and unpredictable, and our decades of studying them have given us truly exciting experiences. In fact, we three authors could have a competition for "peak octopus experience." Was it when Roland watched the giant Pacific octopus (Enteroctopus dofleini) named Olive (she mated with Popeye) tend her eggs until they hatched out in Puget Sound? Or was it when James, as a teenager, thought his self-caught octopus had "escaped" from the tank for three days, and then found it still in the tank but underneath the gravel filter plate? Then there was the event when Jennifer first witnessed tool use by the common octopuses (Octopus vulgaris) of Bermuda. Or maybe it was when Roland, still skeptical about octopus play, phoned Jennifer long-distance after watching an octopus blow jets of water at a floating pill bottle, causing the object to make circuits in its aquarium tank, and said, "She's bouncing the ball!" Perhaps it was when James managed to raise the elusive spoon-arm octopus (Bathypolypus arcticus) for the first time. For all of us, it was also when we looked directly at a camouflaged octopus, realized it looked exactly like the rock behind it, and wondered how the animal could do that. In this book, we share many of these captivating experiences with our readers.

Octopuses are found in most of the habitats in the ocean, and they are an important part of the sea's complex web of life. They do countless interesting things, and in the process challenge how we think about such issues as personality, intelligence, or play, thereby revealing much to us about what it means to be a living being on the earth. But most important, octopuses are wondrous to behold.

The three of us have studied the octopus and its behavior, in the lab and in the field at different locations on the planet, such as Banyuls on the southern coast of France, the islands of Bermuda, the small Caribbean island of Bonaire, and Hawaii. We all started out as what James calls "old-fashioned naturalists," walking and swimming along the shoreline and getting acquainted with what lives there—Jennifer on Vancouver Island, British Columbia, Roland on Puget Sound, Washington, and James in Florida. We started our university educations in biology, getting a foundation in the basics of marine animals, but our paths and major interests diverged somewhat after that.

In graduate school, Jennifer started studying the Caribbean pygmy octopus (Octopus joubini/mercatoris) but switched to psychology, adding an emphasis on theory to her marine biology background. As a university professor, she has explored theoretical ideas in areas such as octopus foraging strategies, personalities, intelligence, and consciousness, and she covers these topics in this book. Roland has worked for the Seattle Aquarium for over thirty years, getting a good grounding in issues of animal care. He's written papers about enrichment for octopuses in captivity, and, in a later part-time doctoral program, he focused on the sand-digging behaviors of stubby squid (Rossia pacifica). His background in these practical areas shows when he discusses many dimensions of octopus life in this book. James completed a doctoral program in biology and oceanography, accomplishing the technically demanding task of keeping the deep-sea spoon-arm octopus and evaluating influences on lifespan. He's on the staff at the Aquarium of the Pacific, in Long Beach, California. Besides becoming an expert on keeping octopuses in aquariums and writing this book's section on the topic, he became interested in the Internet mode of communication, and formed the Web sites The Cephalopod Page and CephBase about living cephalopods. James is also an excellent underwater photographer, and many of the pictures in the book are his.

Together, we hope to help readers understand more about the mysterious marine world and the fascinating octopuses that live in it.

Acknowledgments

We would like to thank Roy Caldwell, John Forsythe, NOAA, Leo Shaw, Barry Shuman, Abel Valdiva, and Stuart Westmorland for providing photographs. We would also like to thank Elena Hannah, Sandra Palm, David Sinn, Kimberley Zeeh, and Brandi Walker for reading and commenting on book chapters. We also would like to thank Leanne Wehlage-Ellis for word processing. Foremost, we would like to acknowledge the octopuses for their inspiration.

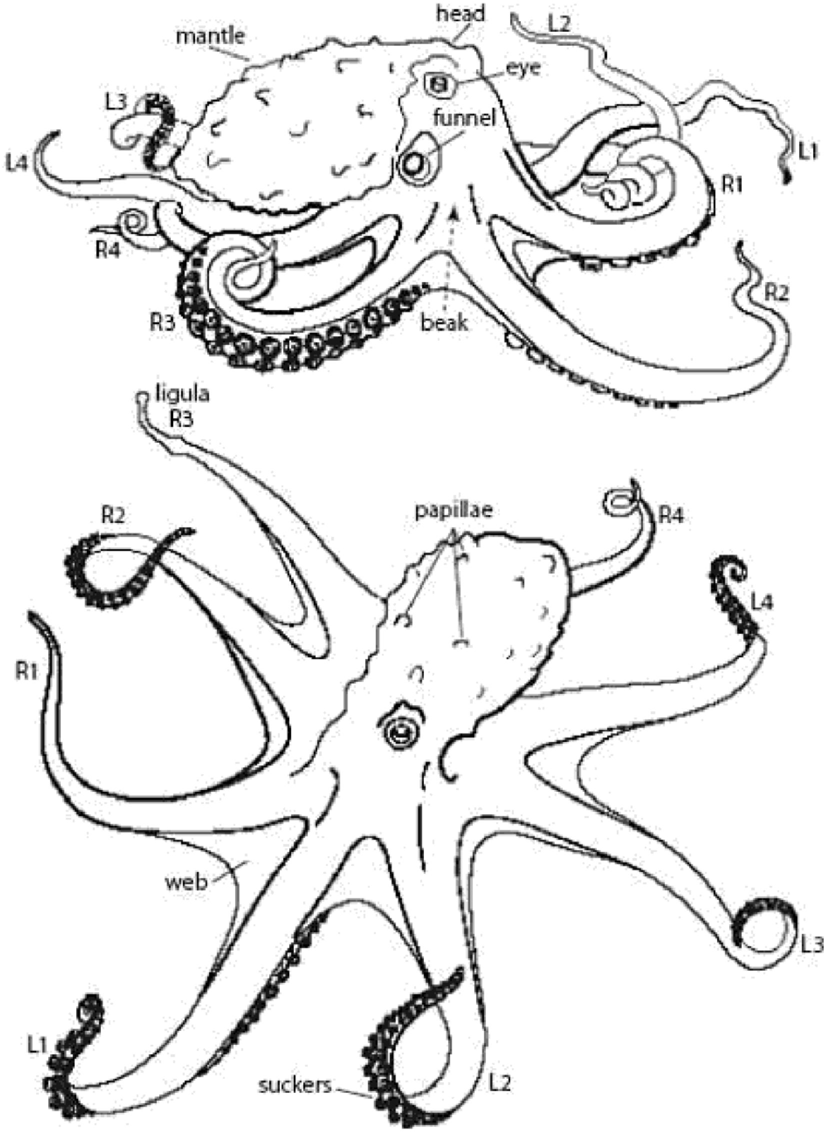
Introduction

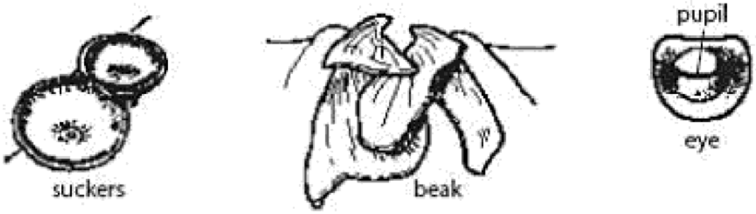
Meet the Octopus

Octopuses are amazing animals. They can change color, texture, and shape. They have three hearts pumping blue copper-based blood, and are jet powered. They can squeeze through the tiniest of cracks and disappear behind a cloud of ink. Octopuses adapt to new situations, solve problems, learn techniques, and are curious about their surroundings. They are considered by many to be the most intelligent of invertebrates. They have the manipulative ability to get into fishermen's crab traps, eat the crabs, and get out again. They can dismantle the aquariums they are kept in, and escape. They can even grow a new arm when one is bitten off.

The octopus is a mollusk, like clams and snails. Through evolution, it has lost the confining but protective shell. Since it is not hidden in the shell, the muscular mantle wrapped around the animals' insides is free to set up jet propulsion—it can contract to shoot water through its flexible funnel (see plate 1). With jet propulsion, the octopus can move through the water, shove aside sand and small rocks to clean out a home, and jet at annoyances like scavenging fish and pesky researchers. The octopus's head is usually raised up high so it can see well through its two lens-type eyes, which are very much like the eyes of mammals and birds except the pupil is a horizontal slit instead of round. The head is surrounded by eight arms that have flexible skin webs between them, and the mouth is underneath at the center of the arms. To name the octopus arms, we divide them into left and right arms by their position compared to a line down the middle of the animal. If an octopus is facing forward with its mantle to the rear, it has four arms on its right and four on the left. These are counted as R1, R2, L1, L2, and so on.

The fluid in the octopus's mantle cavity is an inside part of the outside ocean, vital for respiration and removal of waste. Water circulates around in it as in other mollusks, and its contraction is parallel to our breathing. The tubelike funnel directs the outgoing water after it has passed over the gills and delivered oxygen to the blood, and it expels body wastes in its stream.





External anatomy features of female (above) and male (below) giant Pacific octopus (*Enteroctopus dofleini*). Marjorie C. Leggitt.

Because of this body arrangement, these marine animals are classified as cephalopods ("head-foots" in Latin) and named octopuses because of their eight arms (octopus means "eight-footed"), and they are also bilaterally symmetrical, with left and right sides mirroring each other, like in humans. The third right arm of adult male octopuses is modified to pass spermatophores, or sperm packets, to the female. Because the arms are lined with suckers along the underside, octopuses can grasp anything. And since the animal has no skeleton, it can flex its arms and move them in any direction. The arms aren't tentacles: tentacles are used for prey capture in squid, and these arms, with their flexibility, are used for many different actions.

Octopuses are found in all oceans at every depth and in many different marine habitats. Although we don't know exactly how many species of octopus exist, we think there are approximately 100 members of the genus Octopus, and probably about 300 octopods (members of the order Octopoda) around the world, and some do not yet have common names. Names aren't the only thing missing in the puzzle about octopuses: scientists are still piecing together their behavior, ecology, and physiology. We have seen juvenile common octopuses (Octopus vulgaris) in shallow tide pools in Bermuda and large giant Pacific octopuses (Enteroctopus dofleini) crawling out of the water to get over a rock jetty on the North Pacific coast. Some, such as the spoon-arm octopus (Bathypolypus arcticus), are adapted to the ocean's dark, cold depths up to 3000 ft. (1000 m) below the surface and can be found on the abyssal plain stretching across the bottom of the sea. Hawaiian day octopuses (Octopus cyanea) are found on shallow coral reefs, and argonauts (Argonauta argo) drift in the open ocean. The long-armed Abdopus aculeatus, which has no common name because it is so little known, crawls through near-shore sea grass beds in the eastern Pacific. The specialized deep-sea vent octopus (Vulcanoctopus hydrothermalis) is found, as its name suggests, near deep-sea hydrothermal vents way down at 6000 ft. (2000 m).

Octopuses will eat almost any animal that can't get away from them. Their menu depends on size. Tiny pygmy octopuses eat small hermit crabs, and adult giant Pacific octopuses favor big Dungeness crabs and geoduck clams. They have lots of ways of getting into shelled prey—scraping with their teeth, or radula, grasping with their parrotlike beak, even drilling a hole in the shell of a clam and injecting venom to weaken the muscles so the shell gapes open. The octopus's toxic venom also contains enzymes that start digesting the food. We found that the common octopuses we studied in Bonaire ate seventy-five different animal species. Sifting through the shells of their prey in the midden, or garbage heap, outside their sheltering homes, we discovered that their food ranged from immature conch snails and pen shell clams to shore crabs and shrimp. Some octopuses seem to specialize in one or a few species: the spoon-arm octopus eats brittle stars, one of the few animals common in the deep. Some octopuses have favorite species: the Hawaiian day octopus eats crabs almost exclusively, while the night-active white-striped octopus (Octopus ornatus) in the same islands eats cowry sea snails. All common octopuses adapt, as studies across their huge range have shown, to eating whatever is most easily available where they live.

Surfing the Web for Science

In 2008, Roland completed the data analysis for our study of whether octopuses can remember and recognize individual humans (yes, they can). One measure that distinguished octopuses' reactions to a person who fed them from their reactions to a person who hassled them by touching them with a piece of Astroturf-covered plastic pipe was a specific skin display, the eyebar. The eyebar extends the horizontal line of the octopus's horizontal pupil slit onto the skin on either side of the eye, presumably making the eye look less like an eye. An eye is a dead giveaway that you're facing an animal and not just a piece of the landscape. Many animals manipulate the appearance of the eyes, disguising their real ones or adding fake eyes as displays on the skin, to startle or confuse predators.

All we knew about the eyebar display at that point was that we had seen it when the octopus was annoyed. So I promised Roland that I would look into the structure of the display and its occurrence in different octopus species. How to begin? One situation that qualifies as annoyance to an octopus is being stalked by an underwater photographer, who appears literally in the animal's face, with lots of equipment and trailing streams of bubbles, letting off flash after flash in the octopus's eyes. It's not surprising that when I looked at pictures of octopuses, I saw a large proportion with eyebars.

I gathered photographs of octopuses from colleagues, especially Roland, James, and former graduate student Tatiana Leite, primarily of the common octopus and the giant Pacific octopus. But wanting more, I went to the Web. Finding countless pictures of live octopuses, I selected ones with eyebar displays to enter into my database. I chose the common octopus, the giant Pacific octopus, and the Hawaiian day octopus—species that live in different areas of the world, so that even if the Internet photo description didn't identify the species, I could figure it out from the location where the photo was taken.

After Tatiana ran the photos through a sophisticated data analysis, we found some intriguing things about the display. It's nearly always symmetrical—the line extends on the skin both forward and backward from the eye—and it's painted on the same mottled, pale or red background around the eye. The display is also different among the three species, dark and pencil thin for common octopuses, and wider, delineated by thin white stripes in the other two species. We don't yet know what situations cause octopuses to put the eyebar on their skin, but we do know what it looks like, which is a first step.

This was the first (and probably only) time I've done a research study without leaving my desk.

—Jennifer A. Mather

Even if they get very big, like the giant Pacific octopus, all the group live short lives. The longest octopus lifespan is three to four years, and most of the smaller octopuses die after about six months to a year. Most species start off very tiny, floating in and eating the tiny organisms of the plankton of the upper open ocean, and then they settle to the sea bottom as they get bigger. Young octopuses have only two things on their mind, eating and not getting eaten. They convert food to body muscle and fat very efficiently, partly because they are poikilotherms—they don't spend energy keeping their body warm. At the end of their life cycle, after being solitary animals, octopuses get interested in sex and find each other for mating. After mating, males become senescent and soon die. The female lays from fifty to tens of thousands of eggs, and tends them faithfully, keeping them well oxygenated, clean, and protected from predators. After the eggs hatch, the female dies.

Many octopus babies travel a long distance between the time they hatch and the time they settle to the bottom. Eggs of the smaller octopuses are only about 1/10 in. (3 mm) long. When they hatch, the babies rise to the surface of the water and are washed out to sea or along the shore, floating great distances on marine currents. If they survive, young octopuses eventually get heavy enough that they settle to the bottom, find a likely rocky ledge, muddy bottom, or boulder field, and make a home there. But this isn't true for all octopuses. In California, there are two species of two-spot octopus that look very much alike. One species, Verrill's two-spot octopus (Octopus bimaculatus), lays 20,000 tiny eggs that hatch into planktonic (open-ocean surface) young. But the second species, the Californian two-spot octopus (O. bimaculoides), lays 800 eggs that are five times as long as those of the other species, and when the babies hatch, they are benthic young—they just crawl out and start their life on the bottom of the ocean right away.

Divers and aquarium visitors are fascinated by the octopus's appearance. Octopuses can change what they look like in less than 30 milliseconds by expanding tiny pigment sacs in the skin, chromatophores. They can go from dark to pale, plain to patterned, rough to smooth, and a clumped shape to an elongated form. They change their appearance mostly to hide from predators, camouflaging to match the colors and the patterns of their background. Over brown algae, they will go blotchy brown, on sand they can change to tiny dappled grays and blacks, and under the shade of a rock they can become plum-purple. They can make half of the body pale and the other half dark (see plate 2). And when an octopus is finished matching its background and lifts off to swim away, it can put on a striped pattern, making it harder for a predator to track it. If all else fails, an octopus can squirt out a cloud of ink so the predator loses sight of it.

Although the octopus hides as much as possible to avoid trouble, there is another side to these animals: they can be deadly predators. They can bite into prey with their beak and inject venom from the salivary gland. A small Caribbean pygmy octopus (Octopus joubini/mercatoris) can catch a crab its own weight, and after one quick bite the crab stops moving and in thirty seconds it is dead. One of the most deadly marine animals is the blue-ringed octopus (Hapalochlaena maculosa) of Australia; its venom can be fatal to humans (see plate 3).

What's in a Name?

Throughout this book and in scientific publications, animals are referred to by their scientific names—by genus and species—though we also use common names when they exist. Why not just use common names? The answer is that they are not common, but vary with the location. Think of the robin, quite a different bird in England than in North America, but known by the same common name. In the early eighteenth century, Swedish scientist Carl Linnaeus developed the system of nomenclature for animals and plants, using ancient Latin and Greek linguistics to form binomial scientific names, and it has proved a great blessing for sorting out the diversity of animals and plants. For instance, wherever it occurs, *Octopus vulgaris* is an animal name everyone can understand. And the sorting also tells us about relatedness: every species in the genus *Octopus* is related to others in that genus, and is a bit more distantly related to those in the genus *Enteroctopus*, like *Enteroctopus dofleini*.

How do animals get their scientific names? The scientist who reports a species as a new one has the privilege of naming it or of having it eventually named after him or her. Sometimes an animal is named for a particular feature, like the two-spot octopus, *Octopus bimaculoides*. Sometimes the name refers to where the animal lives; a good example is *Vulcanoctopus infernalis*, which lives around deep-sea volcanic vents. Sometimes the name honors a previous researcher, so *Octopus joubini* is named after French naturalist Louis Joubin, who studied cephalopods in the nineteenth century (*O. joubini* was split into *joubini* and *mercatoris*). Sometimes the name is more whimsical, like *Wunderpus photogenicus*, which was known to divers as very photogenic years before it was described by scientists.

Just because scientific names are useful and commonly used doesn't mean they are fixed in stone; in fact they are fairly changeable. A species is an interbreeding group of animals that doesn't interbreed with other groups, and this can change. Sometimes these taxonomic decisions are challenging for those who are just studying behavior, since it makes us question what species we are working with. I've studied six octopuses over thirty years, and during that time, taxonomists have changed the species name of one of the animals I studied, the genus of another, and we are still not sure of the taxonomic relationships of *Octopus vulgaris*.

—Jennifer A. Mather

A Guide to the Mollusks in the Book

Here are genus and species names for the mollusks discussed in this book, alphabetically within each group, with common names when they exist, based on Mark Norman 2000.

Genus *Octopus*

Octopus abaculus	———
Octopus alpheus	Capricorn night octopus
Octopus bimaculatus	Verrill's two-spot octopus
Octopus bimaculoides	Californian two-spot octopus
Octopus briareus	Caribbean reef octopus
Octopus chierchiae	———
Octopus cyanea	Hawaiian day octopus
Octopus defilippi	Atlantic long-arm octopus
Octopus dierythraeus	red-spot night octopus
Octopus digueti	Diguet's pygmy octopus
Octopus insularis	———
Octopus joubini/mercatoris	Caribbean pygmy octopus
Octopus macropus	white-spotted night octopus
Octopus mimus	———
Octopus ornatus	white-striped octopus
Octopus rubescens	red octopus
Octopus vulgaris	common octopus
Octopus wolfi	star-sucker pygmy octopus
Octopus zonatus	———

Other Members of the Order Octopoda

Abdopus aculeatus	———
Ameloctopus litoralis	banded string-arm octopus
Argonauta argo	argonaut
Bathypolypus arcticus	spoon-arm octopus
Cirrothauma murrayi	blind cirrate octopus
Enteroctopus (Octopus) dofleini	giant Pacific octopus
Grimpella thaumastocheir	velvet octopus
Hapalochlaena maculosa	blue-ringed octopus

Ocythoe tuberculata	football octopus
Opisthoteuthis californiana	flapjack devilfish
Thaumoctopus mimicus	mimic octopus
Vitreledonella richardi	glass octopus
Vulcanoctopus hydrothermalis	deep-sea vent octopus
Wunderpus photogenicus	wunderpus

Other Members of the Class Cephalopoda

Architeuthis dux	giant squid
Cranchia scabra	glass squid
Dosidicus gigas	Humboldt squid
Euprymna scolopes	Hawaiian bobtail squid
Euprymna tasmanica	southern bobtail squid
Heteroteuthis dispar	———
Idiosepius pygmaeus	pygmy squid
Metasepia pfefferi	flamboyant cuttlefish
Nautilus spp.	nautilus
Rossia pacifica	stubby squid
Sepia apama	giant cuttlefish
Sepia latimanus	broadclub cuttlefish
Sepia officinalis	common cuttlefish
Sepioteuthis sepioidea	Caribbean reef squid
Vampyroteuthis infernalis	vampire squid

Other Members of the Phylum Mollusca

Aplysia californica	sea hare
Arca zebra	zebra mussel
Archidoris montereyensis	sea lemon nudibranch
Clione limacina	sea angel
Crepidula fornicata	slipper limpet
Ctenoides spp.	file clam
Humilaria kennerleyi	Kennerley's venus clam
Janthina janthina	janthina
Lima spp.	file clam
Melibe leonina	lion nudibranch
Pinna carnea	pen shell clam
Protothaca staminea	Pacific littleneck clam
Strombus gigas	queen conch
Tegula funebralis	top snail
Venerupis philippinarum	Manila clam

Under this variable skin, an octopus, like other mollusks, has several ganglia, collections of nerve cells that help to regulate activity, spaced around their body. In the octopus, the ganglia are centralized in the brain, which is a large one for invertebrates. Besides these nerve centers, a huge part of the octopus's brain is devoted to controlling the skin display system, and two areas are devoted to storing learned information. We tend to think that nerve cells belong in the brain, but in the octopus three-fifths of the nerve cells are in the arms. They are probably needed there to control the very complicated movement that octopus arms and suckers can make.

The blood of octopuses and other mollusks is blue because of their oxygen-carrying pigment, hemocyanin. Hemocyanin isn't as efficient as our hemoglobin at carrying oxygen. For the slow-moving standard mollusks, that doesn't matter much, but since the octopus's physiology is faster, its circulatory system is modified. The blood is circulated in a closed system, a series of arteries going out to the body and then veins bringing the blood back to the heart, like in humans. Still, this system isn't adequate for the octopus, so the animal has evolved two accessory hearts at the base of the gills that push blood out to get it to the oxygen faster.

Mollusks are in the phylum Mollusca. Since the head-foot group is so different from the snails and clams, they are defined as the class Cephalopoda. Among the cephalopods, there's one really different group, the few species of Nautilus, which are remnants of a huge group that dominated the seas in ancient times; they are slow, live in deep water, and have a scavenging lifestyle. The rest of the cephalopods are the subclass Coleoidea, comprising four orders: true squid, or Teuthoidea; cuttlefish, or Sepioidea and Sepiolida; one deep-sea species of vampire squid, or Vampyromorpha; and the octopuses, or Octopoda. Animals in these four orders have the same basic body plan, though the addition of two elastic tentacles defines the squid as decapods (or ten-footed).

Octopuses face ordinary challenges in unusual ways. Their amazing mobility lets them go almost anywhere they want on the sea bottom to find a hidden crab or snail. The changeable skin allows them to conceal themselves against a wide range of backgrounds or to dazzle a potential mate. They can walk, swim, or pull themselves along the bottom with extraordinary grace, and they can solve problems that other mollusks might not even comprehend. All of these characteristics make octopuses fascinating to study.

In the following chapters, we take you through the life of an octopus. We start with the octopus egg, in chapter 1. Then we describe the issues that matter to an octopus as it goes through the different stages of its existence, and we conclude with mating and the end of life. In the final chapter, we discuss other cephalopods related to octopuses that help us understand the octopus. Then we offer a guide to obtaining and keeping an octopus in an aquarium.

In this book, as authors we refer to each other as "we" or by our first names. Other research findings are cited by first and last author names, and those studies as well as ours are included in the reference list at the back of the book. In the text, you'll find that sometimes the squid is used as the basis of discussion when no good octopus example is known, because squid are similar in structure and physiology.

By the way, the plural of octopus isn't octopi, because the word is Greek—octopous to be exact—not Latin. The Greek plural would be octopodes, but we call them octopuses.

1

In the Egg

Octopuses are oviparous: they lay eggs like chickens do. Some animals are viviparous, like humans: offspring grow inside the mature female, who then gives birth to fully developed young. Other animals are ovoviviparous, like snakes: the female essentially lays eggs inside herself, the eggs hatch inside, and she gives birth to live young. Almost all octopuses lay eggs outside their body and the embryos develop inside the eggs. The process of producing viable eggs and ensuring that the young successfully hatch out is the most important task of a female octopus. This task comes at the end of her life, and she totally devotes herself to it.

The female octopus has two ovaries, where the eggs are produced. As in many other invertebrates or fish, the octopus's ovaries are cream-colored and granular. The ovaries of mature females take up much of the space inside the body: the egg masses may be 25 to 30 percent of the female's weight in some species, like the red octopus (Octopus rubescens), and up to 40 percent in other species. If humans had this high a gonad index, a 120-lb. (55 kg) woman would have a 48-lb. (22-kg) baby!

During mating, the male inserts a spermatophore, or sperm packet, by passing it along its arm to the oviduct of the female. There, the spermatophore turns inside out, the sperm are pushed to the end of the packet nearest the oviduct, and the end of the spermatophore bursts open, releasing the sperm. The sperm are stored in the wall of the oviduct in a special organ, the spermatheca, until they are needed to fertilize eggs. When eggs travel down the oviduct before they are laid, they pass through the spermatheca and get fertilized. We know that live sperm can be stored in the spermatheca for a long time, because, for example, a female giant Pacific octopus was shipped from Tacoma, Washington, to an aquarium in New York City. She was kept alone for seven months and then laid fertile eggs.

Before the female octopus can lay her eggs, she must find a suitable place for them. Most shallow-water octopuses, like common octopuses and Hawaiian day octopuses, lay their eggs in a den. The den might be in a crevice or cave in a rock wall, in an excavation under a rock, or under human-made underwater structures such as concrete blocks, pilings, or shipwrecks. Red octopuses have laid eggs in beer bottles, aluminum soft drink cans, and even in an old shoe. Smaller species of octopuses, such as the Caribbean pygmy octopus, may lay their eggs inside clamshells or even a beer can. And several octopus species carry their eggs with them, not laying them in dens at all. The female argonaut, a pelagic octopus, makes a delicate and minimally coiled shell up to 18 in. (46 cm) across in which to lay her eggs.

If undisturbed, octopus females almost never leave their clutch of eggs. For better protection, a number of shallow-water female octopuses even block up their den openings with rocks, shells, or other material, and don't move the obstructions until the eggs are about to hatch. Hidden dens make it difficult for scientists to find nesting female octopuses and study this important part of their life cycle; Jim Cosgrove (1993), because he has such intimate knowledge of their habitat, has successfully found the dens of nesting giant Pacific octopuses.

Like a chicken's egg, what we call an octopus egg is a complete package, with cushioning material, a yolk for nutrition, and a shell for protection. As a fertilized octopus egg passes down the oviduct getting ready to be laid, it goes through the nidamental gland, where it is coated with a nutritious and protective, clear jelly. It then goes through the oviducal gland, which forms a protective sheath, the chorion, around the egg and its jelly. In some octopus species, the egg is then ready to be laid and guarded by the female. Octopus eggs are typically oval or teardrop shaped, and most are tiny, the size of a grain of rice.

In most octopus species, the chorion is drawn out on one end of the egg to form a stalk. In some species, the female lays large eggs and uses this stalk to attach each egg singly to the ceiling of her den. In other species where the female lays small eggs, a long strand or string is produced by the oviducal gland, and strings of many eggs, up to several hundred, are delicately woven together by the suckers on the female's arms near the mouth to form a festoon of small eggs. Each festoon is then attached individually to the ceiling of the den, forming a cluster. In some species, such as the common octopus or the giant Pacific octopus, there may be hundreds of festoons with tens of thousands of eggs. The female may take more than a month to deposit all these eggs in the den.

The Mysterious Argonaut

Argonauts (*Argonauta argo*) are an enigmatic group of octopuses that are highly specialized. Females begin to build a coiled paper-thin shell like a cornucopia when they are young, and they live in it and lay their eggs in it. They secrete the shell with greatly modified paddle-shaped arms. These arms cover the shell, even when they are swimming. The shell doesn't provide any flotation and these octopuses are good swimmers, living in the open ocean in tropical and subtropical zones, swimming constantly with their water jets to keep them from sinking.

The argonaut was named after the crewmen of the ancient Greek mythological hero Jason, who made epic journeys aboard the ship *Argo*, because argonauts were found "wandering" in all the tropical oceans. The coiled argonaut shell looks somewhat like a nautilus shell, but argonauts are different from chambered nautiluses (*Nautilus* spp.): the shell is part of the body of nautiluses, but female argonauts can leave their shell and then reenter it.

Very little is known about argonauts. We know the eggs are fertilized somehow by pygmy males about an inch long (2.5 cm), which have never been seen in the wild. The males somehow deposit a detached arm containing sperm into a female, and she then uses the sperm to fertilize the eggs. We know little about what argonauts eat, although ones in aquariums have eaten shrimp and small fish. No one has kept them in aquariums longer than about three weeks. Young coming from the tiny eggs, just 1/10 of an inch (2 mm), have never been raised. There is also some indication that argonauts are social. Chains of six to eight argonauts have been photographed, each female holding onto another's shell. We don't know if this was a chance occurrence or deliberate.

We also know little about species of argonauts. They have been identified by characteristics of their shells, largely from those that have washed up on shore, not the actual animal. There appear to be six or eight species with several more undescribed. Norman (2000) tells of a mass stranding he investigated that took place in Australia. Thousand of females with eggs in their shells washed up on the beach, and most of the females and their eggs died. Such mass strandings of argonauts are not uncommon; they may occur from weather or oceanographic conditions.

—Roland C. Anderson

In general, octopuses lay either tens of thousands of tiny eggs or approximately 100 larger eggs, depending on the species. The eggs of the common octopus are about 1/8 in. (3 mm) long, while those of some deep-sea species are more than 1½ in. (40 mm) in length. Each strategy works, or else the species would die off.

Scientists have described the different reproductive strategies of animals in terms of their ecology and life style as a continuum on a scale from r to K. The rate of population increase is the r factor at one end of the scale, and K stands for the carrying capacity of the environment at the other end. Animals using the r strategy mature early at a small size, have a short life span, produce a large number of young with no parental care, and die shortly after reproducing. Animals using the K strategy mature later in life, live longer, produce fewer young with parental care, and can reproduce more than once. Different octopus species fall different places on the r–K line. The r strategy is used by those species producing planktonic young, and those producing benthic young are farther toward the K end of the scale. The deep-sea spoon-arm octopus is one with the highest K value; it produces just a few young and has a relatively long life span of four years or more.

Some species of closely related octopuses are known as sibling species. They appear alike because of their physical features, genetic makeup (or cladistical comparison), and they may even live in the same areas. There are sibling species of zebra-striped octopuses (Octopus chierchiae and O. zonatus) on each side of Panama that were presumably the same species at some time before the isthmus arose. Some of these sibling species have a different place on the r–K line, which also distinguishes them from each other. Sometimes you have to wait until the female lays eggs to know which species of octopus your individual is (see plate 4).

When female octopuses, such as the Caribbean reef octopus (Octopus briareus), put their resources into laying larger eggs, the eggs hatch out larger juveniles that are better prepared to take on the benthic world than their smaller relatives. These larger juveniles are able to crawl, hide, change color, ink, or swim from predators. In other words, they assume a normal subadult octopus life.

We humans use the K strategy. We give birth to just one or a few large offspring, although they are certainly not ready to live by themselves at birth. Anthropocentrically, we may think that having a few large eggs, large offspring, and parental care comprise a good strategy, perhaps the best. This strategy in octopuses produces juveniles that are well able to live an adult life style on the ocean's bottom. But in octopuses, such a strategy prevents a wide dispersion of the species, because they can't get very far from where they grow up: they must crawl or slowly swim to colonize new areas. So they tend to have small ranges, and a species in a small area can be threatened or even wiped out by ecological disasters, such as storms, El Niño currents, or pollution. Examples of this kind of event are the endemic land snails of Hawaii, which have gone extinct from being eaten by another introduced snail; the many freshwater mussels of the Ohio River that have gone extinct from pollution; and the threatened snails in Banff, Canada, that only live in three hot springs. Because of their lack of dispersion, more freshwater and land mollusks have become extinct than all mammals and birds combined.

The other strategy, producing many small eggs and tiny hatchlings, also has its advantages and disadvantages. A primary disadvantage of the production of small hatchlings is that most of them get eaten, although selection means that the fittest survive. Tiny octopus hatchlings look somewhat like miniature octopuses but have stubby arms, an attached yolk sac, and a few chromatophores. They may or may not have inking ability yet. They swim and drift in the plankton until they are large enough to settle to the bottom and take up a usual octopod benthic existence. These planktonic hatchlings are called paralarvae: they don't go through a true larval stage (looking quite unlike the adult), like caterpillars do before becoming butterflies.

In addition to having few resources when they hatch and needing to eat soon, the planktonic paralarvae are likely to be eaten by larger animals that eat plankton. But since there may be thousands of these hatchlings, the chances are good that a few will survive. And since they are planktonic, they are often carried by currents to new areas of settlement. Generally, the more eggs produced by an octopus species, the larger its range, since the paralarvae can float in currents for several months. Production of many eggs may also be good for the gene pool of the species, because it increases the odds of having a variant that might increase survivability.

As far as we know, all female octopuses that lay eggs guard them. They use several methods of protecting the eggs, depending on the species. The football octopus (Ocythoe tuberculata) is the only known octopus that is ovoviviparous: the fertilized eggs are retained in the extended oviducts until they hatch, and the hatchlings are released directly into the water. Since the female argonaut is an open-ocean drifter, she can't use rocks for protection. She secretes a thin calcareous coiled shell with the webs of her first arm pair, inside which she attaches her eggs. She then sits in the shell, protects the eggs from overgrowth by algae, and keeps them clean and oxygenated. She lays the smallest known octopus eggs, just less than 1/10 in. (2 mm) long.

Some deep-sea octopuses have a bigger problem. On the abyssal plain of the deep ocean, there is a thick layer of mud and few hard things to attach eggs to. This mud results from the sediment, plankton, and feces that drift down through the water's layers. So octopuses on the bottom attach their eggs to anything hard they can find: a rock outcrop, a whalebone, a shell, or a shipwreck. A sheet of plastic trawled from the bottom of the North Atlantic had eleven female deep-sea spoon-arm octopuses guarding a total of more than 100 eggs attached to it.

Octopuses give no care to their hatchlings; the females die about the time their eggs hatch. Once the eggs hatch, the paralarvae, or juveniles, are on their own. But females are wonderful at guarding their eggs. They usually find a den that is protected and has good water conditions—high oxygen, low pollutants, and medium water currents. But even members of the same octopus species have different personalities, so this and chance lead them to establish their maternal dens in different areas, sometimes in places that are not very safe.

While the mother octopus tends her eggs, she stops them from getting fouled by overgrowth of marine algae and settling organisms such as hydroids, barnacles, and tunicates that might grow on the eggs (see plate 5). She does this partly by constantly blowing water through her funnel along and between the eggs or egg strands. The festoons are actively moved and bathed by her water jets, so they must be attached securely in order to take this treatment twenty-four hours a day for the about six months it takes for a giant Pacific octopus egg to hatch. She also manipulates the eggs with her arms, grooming them with her suckers and arm tips, which go snaking through the eggs to remove any fungus or algae growth on eggs that might choke or kill them. The egg strings are made of a chitinous, or fingernail-like, material, to hopefully be tough enough to withstand this constant manipulation.

Because the female octopus usually doesn't eat while she is guarding eggs, she may lose up to 50 percent of her body weight during development of the eggs. Not eating while brooding the eggs has several advantages. First, she doesn't foul the den with food wastes or feces, which helps ensure good water quality for the eggs. She certainly could leave the den to find food or eliminate body wastes, but that would mean exposing her eggs and herself to danger from predators. Fish of several species follow foraging octopuses, hoping to snatch a bit of food, and being out eating would advertise a female's whereabouts. Second, she won't produce a midden of shells or other food remains in front of her maternal den. Some octopus predators (including humans) target den middens, finding them by sight or chemical cues. Third, not eating eliminates any chemicals arising from her metabolism or in her feces. Moray eels can find octopuses in their dens, but it is not known yet what chemicals from octopuses they sense. It is possible they sense some product of food metabolism that is not present while female octopuses are guarding eggs, rather than the body tissue metabolism females undergo while brooding.

While she is tending her eggs, the female octopus survives by metabolizing muscle tissues (octopuses don't use fat for metabolism as we do, and have very little fatty tissue), so she deteriorates considerably at the end of her life. She turns gray or pale, as though she can't change color any more. She hardly moves. She shrinks to half her size, and actually looks old and wrinkled. She can open her den if she has blocked it up, and may manipulate the eggs somehow to stimulate them to hatch. If she is guarding small eggs, she will blow the paralarvae out of the den, usually at night, giving them a boost into open water.

Deadly Dedication

In Washington state's Hood Canal, there are several sites known for their giant Pacific octopuses, with rocky outcrops having many crevices suitable for dens. Unfortunately, the waters of Hood Canal experience a period of low oxygen each fall when phytoplankton and macroalgae die, decompose, and use up oxygen in the decomposition process. Oxygen in the water during these periods has been recorded as low as 2 parts per million (ppm), compared to a normal 7 or 9 ppm. Fish and octopuses leave the deep oxygen-starved water and move into the shallows, which have more oxygen for the duration of this event. But dedicated female octopuses guarding eggs can die at the nesting sites, along with their eggs, since they won't leave the eggs. Octopuses move back into the deep water a month or so after this occurrence, either down from the shallows or migrating from other areas.

—Roland C. Anderson

Sometimes females live after their eggs hatch and go into a state of senescence, but this behavior is more commonly seen in males. Senescent octopuses don't hide in a den, but crawl haphazardly over the sea's bottom, unconcerned about predators or prey. Evolution sets a fine balance between the survival of the female and the survival of the eggs; most females live until after the eggs hatch, since dying sooner would be a disaster for the potential progeny.

The egg laying, guarding, and grooming processes have become well-shown by Olive the Octopus, a giant Pacific octopus who laid her eggs at a popular dive site in Seattle's Puget Sound just offshore from the busy downtown area in 2002 (see plate 6). Olive was first seen guarding eggs in Cove 2 near Armeni Park. Divers guessed she weighed approximately 60 lb. (27 kg), based on the size of her largest suckers. A nearby large male octopus had been named Popeye, after the cartoon character, so she was named Olive, after Popeye's girlfriend Olive Oyl. A group of divers dove at the site every Tuesday night and reported their findings to us at the Seattle Aquarium.

Olive made her den under a cluster of sunken wooden pilings called a dolphin. The dive site is an area of ongoing boating activity, and the dolphin may have been tipped over and sunk by a storm or rammed by a boat. The four pilings are bundled together by steel cables and lie on the bottom in 100 ft. (30 m) of water, parallel to shore. She made her den under this dolphin, midway along it, with two openings, one shoreward and one facing toward deep water. Before laying her eggs, she looked out of the deeper opening through the cool 50°F (10°C) water.

There was little evidence of food remains in front of either den opening at the start of her brooding. We have found that the normally hard shells of red rock crabs, a common prey, become thin and fragile within a few days, and those near her den were hard, so she had either just stopped eating or she was reusing a den recently occupied by another octopus. The cluster of sunken pilings had several dens under it along its length. Unlike most other shallow-water octopuses, she did not wall up the entrance to her den with rocks. Instead, she created a fence of 8-in. (20-cm) rocks in a semicircle in front of the deeper opening, and she didn't put anything in front of the shoreward one. During her entire brooding period, she was highly visible to hundreds of divers.

Divers first saw her eggs on February 25, 2002. She laid the characteristic strings of eggs on the ceiling of her den, attached to the underside of the wooden pilings. That day, she was observed in an upside-down posture with her suckers facing upward, so it is likely she was still in the process of laying eggs. No one counted the eggs, but giant Pacific octopuses characteristically lay about 70,000 eggs. Larger females lay more eggs and smaller ones lay fewer. Olive was a bit larger than normal, so she may have laid about 100,000 eggs.

On later dives in following weeks, divers saw her right side up, blowing water through the eggs and caressing them with her arm tips. At this time, she was normally a dull gray color, but she turned red-brown in response to divers' bright underwater lights or a gentle touch. During the month after the eggs were seen, she would take a piece of herring offered as food by divers, but later she wouldn't eat, and blew offered food assertively out of the den.

She guarded her eggs through the summer, seemingly unfazed by the hundreds of divers viewing her. She pushed sunflower sea stars away from her brood chamber and fended off other egg predators that hovered nearby. She ignored octopuses that made short-term dens nearby under the dolphin, even when they mated as close as 50 ft. (15 m) away. She probably didn't notice their absence as they moved away, the female to make another maternal den of her own somewhere else and the male going off to die.

During that summer, Olive behaved normally for a giant Pacific octopus guarding eggs: she refused food, she was never seen out of her den, she constantly kept the eggs clean, she repelled predators and egg eaters, and she grew unresponsive to divers, maintaining a gray color that gradually turned to a translucent white. Her eggs were white when first laid, but gradually changed to a yellow color as the embryos grew within, and then turned brown with chromatophores just before hatching. Divers saw eyespots inside the eggs in mid June, about 110 days after the eggs were laid, so they knew the eggs were fertile.

Divers witnessed the first of Olive's eggs hatching on a night dive on September 22, 209 days after the eggs were laid. While a few of the paralarvae swam out of the den during the daytime, Olive blew most of them out of the den at night. She may have been causing them to hatch at night by blowing strong water jets over them. At this point, she was totally white, almost translucent. Her skin had several large white ulcers on her arms and mantle, and it had the appearance of rotting away. She was totally unresponsive to divers, even when touched, devoting her remaining energy to her eggs.

The peak of the paralarval hatching was October 7, 224 days after she laid her eggs. Divers saw the last hatchlings on October 31, and at that time there were virtually no eggs left unhatched. Olive was dead on November 6, 254 days after laying her first eggs. Her body was about 6 ft. (2 m) from the opening of her den, being fed on by two sea stars. Nothing goes to waste in the sea, and scavengers are always waiting for the chance to clean up dead bodies.

The precise timing of her death to the last hatching of her eggs is remarkable. Although it sounds anthropocentric, it looked as though she clung to life until she knew her eggs hatched. It is also remarkable that she was able to bring her eggs to successful hatching considering her circumstances. Her den was located within Seattle's inner harbor, next to the outlet of a river that flows through an industrial area. The river and the harbor were once very polluted. Her success may be a testament to our modern pollution clean up efforts and awareness of the necessity of keeping pollutants out of rivers and bays, or it may simply reflect the durability of this female and her eggs.

Olive was visited almost daily by curious divers. Her home was Washington state's most popular dive site, used by many dive classes as their first open-water dive each week, since the location is sheltered from storms and their waves. Her success despite all these disturbances is also a testimonial to her dedication to the eggs.

The saga of Olive the Octopus brooding her eggs in Seattle's harbor was covered by several local newspapers and magazines. The reading public was entranced with her story and saddened by her death. The diving community also mourned her death. One dive magazine ran an article about her, "So Long, Olive, We Barely Knew You," lamenting the short life span of octopuses.

Many octopus eggs take a long time to develop. While the 224 days Olive's eggs took to hatch is a bit more than the about six months reported for the species, this egg development period is by no means the longest for an octopus species. Egg development time is dependent on the temperature of the water: the colder the water, the longer the development period within the egg. Eggs of the giant Pacific octopus in California have a four-month development, while those in Seattle or Alaska may take seven to eight months to hatch. The spoon-arm octopus of the North Atlantic and the Arctic Ocean lives on the continental slope, in water that is 600 to 1200 ft. (200 to 400 m) deep and a temperature of about 35°F (2°C). James has raised this type of little octopus through several generations, and he has found that their eggs take over a year to hatch out into benthic juveniles, ready to take up the bottom-dwelling existence of their parents.

Most deep-water octopuses have large eggs with long development periods that hatch out looking like their parents. This is logical when you consider where they live. There is nothing small like plankton in the ocean depths for the paralarvae to eat, so they must be large enough to be able to eat larger organisms. Some moderately deep-water fish spawn eggs that float to the surface waters, where their hatchlings live in the plankton, only to swim deeper when they are older and large enough to undertake such a vertical migration. But they may only migrate down a thousand feet or so. Other deeper-living fish and octopuses don't use this risky strategy, nor do most other creatures that live a mile deep.

Biologists Janet Voight and Tony Grehan, filming a rocky outcrop rising above the muddy abyssal plain off the west coast of Canada from a submersible in 2000, made a fascinating discovery: they saw twenty-eight female octopuses (of unknown deep-water species) guarding eggs laid on the rocks. They had laid eggs in different places and each had laid fewer than 100 large eggs, attached singly to the rocks. Some of these eggs were the largest known of any octopus, about 2 in. (5 cm) long. After some of these eggs were collected, they hatched out into the largest octopus hatchlings known to science. One female was still guarding her eggs in the same location a year later, and she looked senescent the second year, much like Olive toward the end of her brooding period. Based on the rate of development of the eggs, their size, and the temperature of the water at those depths, we believe it may take up to four years for the eggs of this species to hatch, presumably guarded all the time by a fasting female octopus. At least the deep-water females don't have as many predators to watch for as the shallow-water species do, but the brood time is remarkable. The possibility that the female doesn't eat during such a long guarding period is something to think about, and extrapolation from the brooding time leads to a possible life span of that species of over ten years, the longest for any octopus. Everything's slower in the deep.

Researchers have collected developing octopus eggs and viewed them under light with low-power microscopes or opened them up to see several stages of the development that occurs inside the egg. Huge changes take place in the egg capsule, starting with a cell and ending up with a complete and fairly well-developed animal. Since the egg capsules are usually opaque, embryologists (who study development before birth) can sometimes see what's going on inside, but often they have to open up an egg, preserve the embryo, and study it later. The single fertilized egg cell divides into clumps of cells, arranged in blastula and then gastrula stages. Gradually these cell collections begin to specialize, and we can see the beginning of the adult organs. Meanwhile, the little embryo flips its position in the egg twice, ending up with its mantle pressed against the opposite end from the attachment, ready to push out in the world during hatching.

When does an egg become an octopus? The changes are gradual; there's no specific time, as in all embryological development. First, the yolk develops to nourish the embryo and can be seen extending toward the egg capsule attachment. Then the arms develop, first visible as eight arm buds around the yolk and gradually getting longer (though the planktonic octopuses like the giant Pacific octopus don't have very long arms at birth). The eyes begin to develop at this point, and since they are dark with their pigment, anxious aquarists and the divers visiting Olive could see them through the capsule and know the eggs had been fertilized. Next, the heart begins to develop well enough to be an organ and to beat. The final part of the octopus that can be seen to develop is the chromatophores—there are not many of them and they are conspicuously large in the semitransparent skin. All through the embryonic period, the yolk is used to nourish the embryo, and by the time of hatching, none is left. Sometimes an octopus is disturbed during her brooding, and she may inadvertently push the eggs around so they hatch early. If so, they will have remains of the yolk sac like a deflated balloon sticking out from between their arms.

Hatching must be a traumatic event in the life of the octopus embryo, just as being born is to humans. We go from being cushioned, warmed, protected, and nourished by our mothers inside their bodies to living by ourselves. We go from not having to breathe to having to expel liquid from our lungs and drawing our first breath. Through the course of vigorous muscular contractions, we are expelled out the birth canal into the external world, much like other mammal babies. Chickens and other birds have to chip their way out of their tough eggs. Frequently the chicks have a hatching tooth that helps them penetrate the eggshell, which is later resorbed or falls off as the chick grows up. Some reptile mothers such as crocodiles help the eggs hatch by gently cracking the eggs, and mother octopuses may also help the eggs hatch.

Octopus hatching occurs with the aid of a hatching gland, a collection of enzyme-containing cells on the mantle of the embryo that help dissolve the chorion (egg shell), along with violent expansions and contractions of the mantle. The little octopus paralarva breaks mantle-first through the distal end of the egg, popping out in the normal swimming posture of a jetting octopus. The octopus lives on a remnant of its yolk sac for the first few days, but that is soon absorbed, and the hatchling must find food for itself. Benthic hatchlings, like those of the Caribbean reef or Californian two-spot octopus, just crawl away, but paralarvae of species such as the red octopus take up the life style of a drifter, swimming in the rich surface waters of the sea.

2

Drifting and Settling

While most octopuses live on the sea bottom, the situation is different for the newly hatched young. The many species of octopuses have two different life style strategies as hatchlings. These differences come from the size of the eggs, not the size of the adult animals: the giant Pacific octopus is one of the biggest octopuses but has tiny young. Most octopus species lay small eggs that produce small baby octopuses that are planktonic—they get washed away by ocean currents and temporarily live in the plankton-rich surface waters of the ocean. A few species lay large eggs that produce benthic hatchlings, big enough to live on or near the bottom of the ocean.

Living in the plankton requires adaptations, especially for the early stages of an animal like the octopus that later spends its adult life crawling on the bottom of the ocean among the rocks or coral. To understand why many young octopuses start their lives in the plankton, we must understand what plankton is, how the plants and animals that comprise plankton live, what methods they use to keep from sinking, what they eat, how they swim, what preys on them, and how they avoid being eaten. We must understand the advantages and disadvantages of living in the plankton, the bigger ecological implications of having a life stage different from that of an adult, and the adaptations and changes needed to live that life stage in that environment.

The word "plankton" is derived from the Greek root word that means free floating or wandering. The term is applied to any plant or animal that is unattached and floating in the surface waters of the ocean as well as to any weak, swimming animal that cannot swim against the ocean's currents. Even some comparatively large creatures such as jellyfish and the open-ocean argonaut octopus are part of the plankton. Relatively huge creatures such as sea turtles and ocean sunfish, which are weak swimmers, are sometimes considered planktonic. Plankton includes marine bacteria, animals, and plants, and some swimming animals that have plant pigments that undergo photosynthesis (making food from carbon and oxygen), which is normally a plant trait.

In her poem Plankton, Joan Swift wrote:

> They live their lives unseen
> Not just gray mobs without faces
> But like calm, steady workers
> In some underground plot
> To keep the world alive.

Plankton does indeed keep the world alive and is pretty much unseen and under-appreciated.

Animals and plants living in the plankton are the most important organisms in the ocean, but they are neither the most visible, the best known, the most highly beloved, nor the most feared. They are not the whales, the sharks, or the sea stars. They are not the familiar animals we eat, such as clams or oysters. They are not the organisms we mostly study, like porpoises, or the animals we capture to exhibit in public aquariums. They are usually not octopuses, although some octopuses are part of plankton as juveniles and a few as adults. In The Log from the Sea of Cortez (1951), writer John Steinbeck said that the disappearance of plankton, although the components are microscopic, would in a short time probably eliminate every living thing in the sea and ultimately the whole of human life. Since he wrote that, we have learned of the ecological communities surrounding the deep-sea hydrothermal vents that are not dependent on plankton for their survival, but instead depend on the hydrogen sulfide there, and they use bacteria to break it down and gain energy. But everything else in the ocean depends on plankton.

Plankton can be divided into plants (phytoplankton) and animals (zooplankton). Most animal phyla have representatives in the plankton, at least at some stage of their lives, since many animals such as fish and octopuses spend their juvenile stages there. Those creatures that are only in plankton temporarily are known as meroplankton, such as octopus paralarvae, while those that spend their whole lives there are called holoplankton, such as small single-celled plants, or diatoms.

The animals and plants of the plankton are extremely important to the ecology of the oceans. First, the plankton provides food for most of the ocean's other animals. Phytoplankton provide food for zooplankton, which in turn are eaten by fish and by other tiny organisms like paralarval octopuses. Little fish are eaten by big fish, and fish are eaten by sea birds, squid, marine mammals, and humans. The world's largest fish, the whale shark, and the world's largest animal, the blue whale, both live on plankton. Dead plankton and their waste products drift down to provide food for mid-water animals and those living on the abyssal bottom. The numbers of animals and plants in the plankton are tremendous. Terrestrial insects represent the most species (over a million have been described), but there are more copepods, small weak-swimming crustaceans, in the ocean than any other animal on earth.

Counting Copepods

I got an idea of how many plankton there are when I was an undergraduate at the University of Washington in Seattle. As part of the laboratory experience in a biological oceanography class, we had to separate a plankton sample into its constituent parts, to species level. The sample came from the Chukchi Sea, northwest of Alaska. It was almost all copepods, collected with a large plankton net towed behind the oceanographic research vessel *Thomas G. Thompson*.

The sample consisted of a quart-sized jar filled with microscopic organisms. I don't remember how long a plankton tow this represented or how much water was strained to get this amount of plankton. The plankton was divided into equal portions for each member of the class. The class was not large, maybe a dozen students, and we each had to separate our sample into six species. My sample was in a specimen bottle about the size of my middle finger and was filled with copepods. After several full afternoons poring over a microscope and breathing formalin, we ended up with smaller specimen jars, each with a precise number of different species.

This tedious chore gave us a valuable experience in the field of taxonomy, the science of zoology that divides animals into species. And the exercise gave the principal investigator on the staff an idea of water conditions where the sample was taken, since different species live in different conditions.

Copepods are the most numerous animals on Earth, and they are very important. Large planktivores such as whales eat them, as do juvenile octopuses drifting in the plankton the first few months of their lives.

—Roland C. Anderson

Second, a huge part of plankton is made up of plants or other organisms that have chlorophyll and produce their own food. As a side effect of this process, the oceans produce 50 percent of the oxygen in the earth's atmosphere, 95 percent of which comes from phytoplankton and 5 percent from bigger algae (kelp and seaweed) or the few marine vascular plants that live near shore. These organisms also provide habitat for marine animals, like mature octopuses and their prey. At the same time, the plankton absorbs carbon dioxide and uses it for metabolism. Because of the large volume and surface area of the oceans, two thirds of the earth, this activity provides an enormous buffer to the oxygen–carbon dioxide budget of the earth's atmosphere. Carbon dioxide is currently increasing in the earth's air despite this buffer, because we humans create huge amounts of it. Plants on land and in the sea can't keep up with our industrial emissions. Plankton may also lessen the atmospheric ozone layer that contributes to global warming and bleaches the coral habitats in which many octopuses live. Clearly, the plankton in the oceans is immeasurably important for our survival.

Third, plankton is important as an energy source. Dead plankton falls to the ocean bottom and collects there slowly, under ½ in. (1 cm) in 1000 years but amounting to thick deposits over millions of years. The rich oil deposits around the Gulf of Mexico are the result of plankton deposits on the floor of an ancient sea there millions of years ago. While it's a harsh environment, some specialized octopuses such as the spoon-arm octopus live there.

Fourth, both live and dead plankton can be ecological indicators. There are some plankton that exist only under specific climatic conditions and some that behave differently at different temperatures. By looking at fossil plankton, scientists can tell what the climate was in the past. For example, some foraminiferans, which are plankton with tiny, coiled shells, shape their shells in one direction in cold water and in the opposite direction in warm water. The percentage of left-to-right coiled fossil forms of these plankton in the ocean's sediments can tell us the sea's temperature at a particular time in the earth's history (see plate 7).

An example of how plankton balance can go wrong occurred in the 1960s. Lake Washington, an urban lake in Seattle, was becoming eutrophic: it was so rich from fertilizers in runoff and sewage that a blue-green alga bloomed in the freshwater plankton. That alga flourished, taking nutrients away from normal plankton, clogging the gills of fish, and reducing the clarity of the lake, so other organisms in the lake suffered. Swimming areas were closed. The lake was well on the way to becoming a muddy, sterile body of water, much like Long Island Sound is today, with few fish and green growing plants. Based on dire predictions of scientists monitoring the situation, the surrounding community was able to stop the processes leading to eutrophication by diverting sewage and runoff. Lake Washington is now a scientific success story: instead of being a turbid, dead lake, it is clean and clear, and the plankton are back to their normal state.

Fifth, plankton can be lethal, even to some of the organisms that eat it. Or the plankton's poison can be collected by and concentrated in the animals that eat it. One classic example is paralytic shellfish poisoning (PSP), or "red tide." PSP happens because filter-feeding shellfish we eat, like mussels, clams, and oysters, collect the poisonous plankton. Carnivorous octopuses don't accumulate these poisons and so aren't poisonous to humans. The organisms that cause PSP are one of those pesky groups that seem to be both animal and plant, and they bloom in such huge numbers, they cause the water to be a rust-red color. In 1793, while exploring the North American West Coast, the crew of explorer Captain George Vancouver ate some mussels from the shores of British Columbia. Four of the crew became sick, suffering numbness and tingling of the arms and legs followed by paralysis, and one died. In modern times, few people are affected by PSP, since commercial shellfish harvests come from safe water and at safe times, and the public is notified of red tide blooms. Red tides usually occur in the summer: there's an old, usually reliable adage that says to only eat oysters in months with an R in them. Red tide can kill marine animals too; a red tide bloom off the coast of Florida recently eliminated a local population of pygmy octopuses that ate infected shellfish.

While dead plankton and its waste products are constantly falling down through the ocean to the bottom, continually adding to the sediment, living plankton must remain in the rich, well-lighted surface layers. This is particularly important for a plant or an animal with chlorophyll, which needs the energy of sunlight to drive photosynthesis. Light is absorbed in the upper 1000 feet (300 m) of the ocean, and the lower depths are essentially black.

Although plants and animals of the plankton, including cephalopods, use several methods to stay near the surface, many members of the plankton have no special adaptations for staying afloat. They slowly sink down through the ocean's surface layers and die when they get too deep to photosynthesize or find food. But they are fast and prolific spawners, and they reproduce before they sink too deep. Their eggs and sperm are buoyant, so they float to the surface, where fertilization takes place and the whole life cycle begins anew. Organisms that go through this cycle (such as diatoms) are usually small.

Other planktonic organisms are adapted in some way to making themselves buoyant or to hover, maintaining their position. These adaptations can either be active or passive. One common passive method is to increase the ratio of the area of the outer surface to the volume, thus making the animal or plant more buoyant or likely to sink more slowly: for example, some organisms have spines or other projections on the outer surface that provide resistance to falling through the water. Octopus paralarvae have bundles of bristles, Kölliker's organs, sticking out of the skin that may do this. And, paralarval Atlantic long-arm octopuses (Octopus defilippi), which have a specialized, long, third arm pair, can extend these arms and drift in the surface waters. Planktonic octopus paralarvae with these adaptations look a bit different from the adults, but they are still recognizable as octopuses.

Another way members of the plankton increase buoyancy is to produce a substance that is lighter than water and retain it in their tissues. Many animals and plants of the plankton do this by secreting a type of oil, and oil is lighter than water. This oil eventually winds up as the hydrocarbons of petroleum deposits. The oil-rich blubber of whales helps offset the sinking of the whales' heavy bodies and also keeps them insulated from the cold. Many planktonic organisms have oil globules in their cells, which are visible when they are examined under a microscope.

Another substance used to keep plankton buoyant is ammonia, again lighter than water. Ammonia is primarily used by the large squid species, including the giant squid (Architeuthis dux), in their tissues, although the glass squid (Cranchia scabra) concentrates ammonia inside a special organ. The ammonia in the tissues of these squid makes the living or dead animals smell pungent. Dead or dying giant squid floating on the ocean's surface smell particularly foul. The ammonia in these giant squid also makes them inedible—there will be no giant squid calamari. Clyde Roper (1984), expert on the giant squid, once sampled a cooked piece of this monster and remarked that it was really terrible tasting stuff.

Other sea creatures use jelly and air as flotation substances. The mesoglea, or jelly layer, of jellyfish helps them maintain their buoyancy. We have been recently finding many new deep-water species of jellyfish, which, even though they are light, have to swim to keep from sinking to the bottom. Some jellyfish use air for flotation, such as the Portuguese men-of-war, as do some cephalopods (such as cuttlefish and nautiluses), fish, and marine mammals. Cuttlefish have an internal shell of porous air-retaining calcium, a cuttlebone, and nautiluses have a coiled shell with air-filled chambers.

Another trick to increase buoyancy is to decrease the density of one's tissues. The few mid-water cephalopods, those that live just above the deep bottom, are usually gelatinous, with tissues close to the density of the deep water they live in. The flapjack devilfish (Opisthoteuthis californiana) and other octopuses like it are sometimes called jellyfish octopuses, because their flabby, gelatinous bodies remind researchers of jellyfish.

Many of the planktonic animals, including young octopuses, swim to maintain their level in the ocean. The methods of swimming are as diverse as the planktonic organisms themselves. Some general methods include beating of the hairlike cilia, thrashing with one or several whiplike flagella, paddling with fins or feet, pulsing, oscillation or undulations of the whole body, or the jet propulsion used by paralarval octopuses. Hatchling octopuses, like squid, may use jet propulsion to raise them in the water column, and then take a long glide to rest before pumping again.

are the same species as in the Caribbean, though fewer. Also, the planktonic offspring from marine animals living in Bermuda are carried northward, often dying in the colder waters or unable to find a place to settle. Some live because they are caught in local currents and stay in the warm bays of the islands themselves. They have to land on an island or a continent to live.

Hawaii, on the other hand, sits in the mid Pacific, isolated in the center of a mid-oceanic gyre of ocean currents that circle these islands. As a consequence, plankton including young octopuses tend to stay in the area, and currents from other islands rarely reach Hawaii. According to the theories of biogeography—essentially why an animal lives at which places—Hawaii should then have a high percentage of endemic animals (those only found there), including octopuses, and it does. Because of the currents circling the islands, planktonic offspring from several octopus species remain there rather than getting carried elsewhere or lost.

Living in the plankton exposes the octopus paralarvae to a great chance of getting eaten because there's no place to hide, and they do get eaten. Out of the 50,000 eggs laid by a common octopus, it only takes one male and one female hatchling to survive in order to reproduce and maintain the species. And, in fact, if more survived, the ocean would be awash with octopuses.

Predators in the plankton are varied in their methods of catching and eating prey. Jellyfish trail out their long tentacles that are studded with lethal stinging cells. Schools of millions of fish, like herring, snap up billions of planktonic animals each day. Large whales consume plankton like a vacuum cleaner sucks up dust. To get an idea of how menacing these planktivores are, picture a paralarval octopus, just ¼ in. (0.6 cm) long, as a potential meal for a typical jellyfish, 3 ft. (1 m) across with tentacles up to 60 ft. (18 m) long. Such large animals as jellyfish, whales, or whale sharks eat tremendous numbers of tiny planktonic animals just to survive, including the tiny paralarval octopus.

But the large planktivores are not the main predators of plankton animals. That distinction belongs to arrow worms, which are not worms at all but are members of their own phylum, Chaetognatha. The second most abundant animal group in the sea, they are about 1 in. (2.5 cm) long and have paired fins and a tail for swimming. They have eyes and cilia for detecting their prey, mostly tiny crustaceans called copepods, which they grasp with spiny

Index