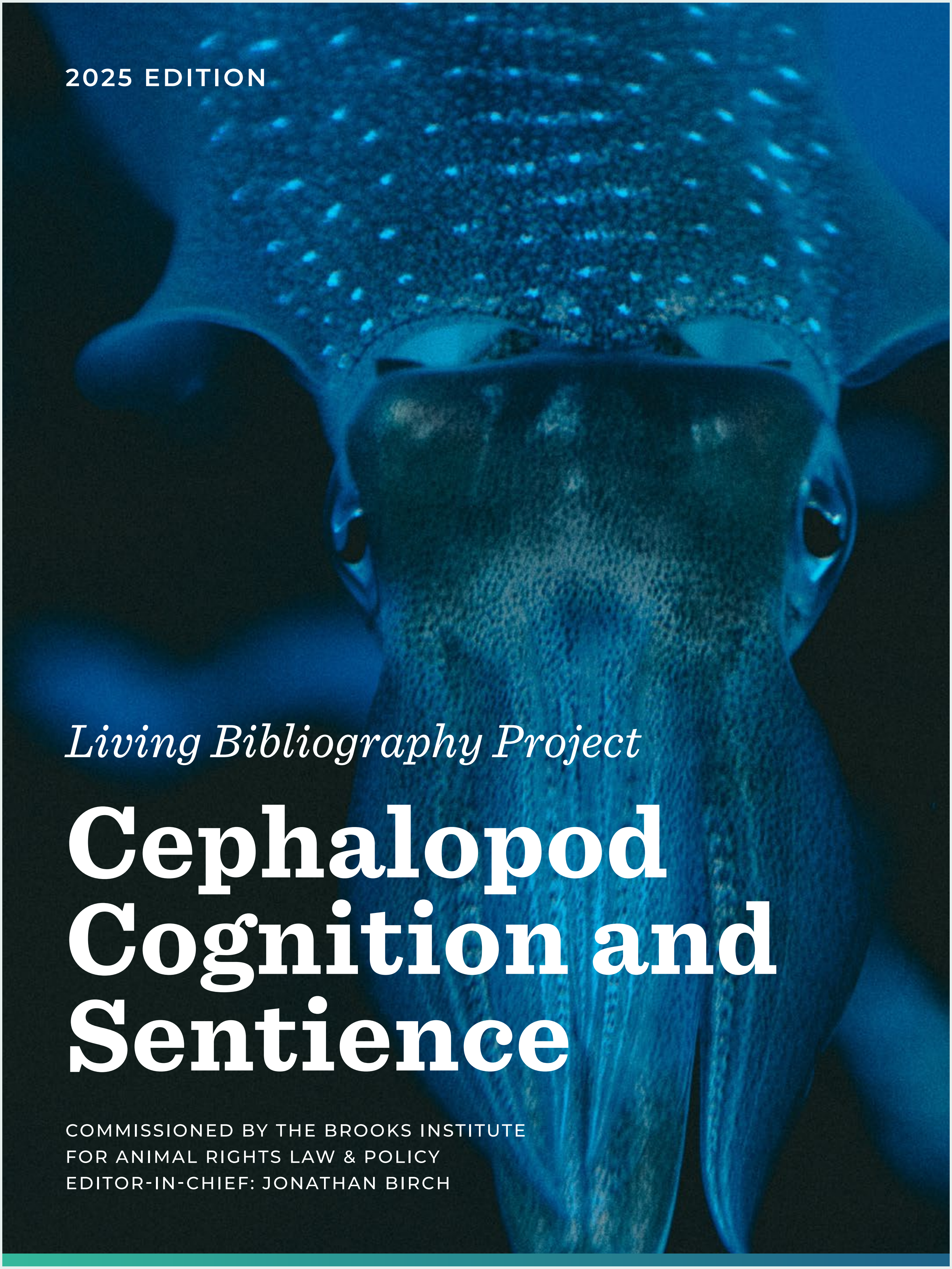

2025 EDITION

Living Bibliography Project

Cephalopod Cognition and Sentience

COMMISSIONED BY THE BROOKS INSTITUTE
FOR ANIMAL RIGHTS LAW & POLICY
EDITOR-IN-CHIEF: JONATHAN BIRCH

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About the Editors

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Jonathan Birch is a professor of philosophy at the London School of Economics and Political Science (LSE) and principal investigator on the Foundations of Animal Sentience project. He mainly works on animal sentience, cognition, and welfare and the evolution of altruism and social behavior.

He joined the LSE in 2014. Before moving to London, he was a junior research fellow at Christ's College, Cambridge. He completed his PhD at the University of Cambridge in 2013, with a dissertation entitled "Kin Selection: A Philosophical Analysis." In 2014, he was one of four UK philosophers honored with a Philip Leverhulme Prize, which recognizes "the achievement of outstanding researchers whose work has already attracted international recognition and whose future career is exceptionally promising".

He has published widely on various topics in major philosophical and scientific journals, including *Nature Medicine*, *Current Biology*, *Trends in Cognitive Sciences*, *The American Naturalist*, *Biological Reviews*, *Nous*, *Philosophical Studies*, *Philosophical Quarterly*, *Philosophy of Science*, and *The British Journal for the Philosophy of Science*. His first book, *The Philosophy of Social Evolution*, was published by Oxford University Press in 2017.

In 2021, he led a "Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans" that led to invertebrate animals including octopuses, crabs, and lobsters being included in the UK government's Animal Welfare (Sentience) Act 2022. His second book, *The Edge of Sentience: Risk and Precaution in Humans, Other Animals, and AI,* was published by Oxford University Press in summer 2024.

Peter Morse

Dr. Peter Morse is a freelance researcher, currently specializing in the role of sexual selection in the evolution of animal intelligence. Peter attended the University of Western Australia (UWA) from 2004–2007, completing a double major in zoology and marine biology and earning the Harry Waring Memorial Prize in Zoology. In 2008, Peter continued at UWA to undertake an honours thesis, “Female Mating Preference, Polyandry and Paternity Bias in the Gloomy Octopus (*Octopus tetricus*),” which addressed intra-specific signaling of cephalopods using polarized light, and postcopulatory fertilization mechanisms in octopus. Peter graduated with first class honours and was awarded the Ernest Hodgkin Memorial Prize in Marine Science. Peter went on to spend the next four years traveling and working as an environmental consultant, tour guide, bartender, and dive instructor.

In 2012, Peter commenced a PhD in zoology with James Cook University and the Australian Institute of Marine Science. His thesis was entitled “The Behavioural and Molecular Ecologies of the Southern Blue-Ringed Octopus (*Hapalochlaena maculosa*)” and focused on the reproductive biology and genetic structuring of an endemic Australian octopus species possessing a unique life-history. This research showcased novel hypotheses regarding cryptic female choice in octopuses, the wide-spread evolution of polyandry in cephalopods, and the overall complexity of cephalopod mating systems and its role as a genetic driver for sophisticated cognition within this invertebrate lineage.

After completing the PhD in 2017, Peter relocated to Cape Town, South Africa, where he began collaborating with a non-government organization, Oceans Research. There, Peter temporarily refocused his research on the predatory behavior and conservation of white sharks (*Carcharodon carcharias*). In 2019, Peter returned to Australia and began working as a postdoctoral research fellow for the Australian Institute of Marine Science, focusing on the conservation of marine megafauna.

Peter is an Australian, US, and Austrian national. However, he currently resides in Florianopolis, Brazil, where he guest lectures at the Universidade Federal de Santa Catarina, follows his passion for underwater photography, and attempts to write a book.

Alexandra K. Schnell

Dr. Alexandra K. Schnell is a comparative animal psychologist, National Geographic Explorer, and visiting scholar at the University of Cambridge, where she also previously served as a research associate. An accomplished academic and expert in animal behavior and psychology, her research spans cephalopods, corvids, and fish. Alex holds a bachelor's degree in marine science from the University of Sydney and completed her PhD at Macquarie University, where she collaborated with the Marine Predator Research Group to explore cuttlefish behavior.

Her current research investigates the cognitive abilities of cephalopods, with a focus on whether these large-brained marine molluscs exhibit intelligence comparable to advanced vertebrates. Comparative studies across such distantly related species offer unique insights into the evolutionary origins of complex cognition, including the roots of human intelligence.

Alex's extensive career includes creating animal behavior content for natural history documentaries and peer-reviewed publications. She combines academic insight with practical experience in production and on-screen roles, most recently as the producer and host of

National Geographic's *Secrets of the Octopus*, where she brings the wonders of marine life to audiences worldwide. Passionate about inspiring others to connect with nature, Alex's work seeks to foster an appreciation for the extraordinary behaviors of non-human animals, promoting conservation through understanding.

Piero Amodio

Dr. Piero Amodio is a permanent staff scientist at the Stazione Zoologica Anton Dohrn (SZN) in Napoli, Italy, and a National Geographic Explorer. He studies the behavior of other species, both in the lab and in the field, as a tool to unravel fundamental aspects of the mind and evolution of nonhuman animals.

He holds a PhD in psychology (University of Cambridge, 2020), MSc in anthropology (University of Zurich, 2015), and MSc in animal behavior (University of Firenze, 2013). After completing his studies, he joined the SZN as postdoctoral researcher funded by the Leverhulme Trust, and in 2022 he was appointed as principal investigator.

Piero has worked on primates, corvids, and cephalopods, publishing on various topics, including camouflage, predatory behavior, complex social cognition, future planning, tool use, mirror self-recognition, and cognitive evolution. His research has received coverage from international media such as *The New York Times* and *The Atlantic*.

About the Living Bibliography Project

The Living Bibliography Project is a first-of-its-kind authoritative, curated synthesis and listing of all the best scientific reports and studies on the sentience and cognition of selected animal species—kept current and relevant—for the purpose of advancing animal interests. This report is the inaugural volume in the series, commissioned by the Brooks Institute for Animal Law and Policy and authored by Jonathan Birch (editor-in-chief), Peter Morse, Alexandra K. Schnell, and Piero Amodio. The authors believe this work to be current as of January 2025.

Overarching Methodology

The Brooks Institute is pursuing an effort to advance animal law and policy through the use of science and effective communication. Our goal is to create new bridges between law, science, and advocacy that prompt a paradigm shift for nonhuman animal protection. Our methodology calls for the collection, collation, integration, and synthesis of scientific studies in nonhuman animal sentience, cognition, and agency. Through this initiative, the important roles that nonhuman animals play in society and culture will hopefully be recognized and a higher moral understanding of nonhuman animals will emerge. We believe this philosophical evolution will form the basis for—and support—legal change, moving the field of animal law away from a property paradigm to a protection and rights paradigm.

Citable Authority

Our goal is to create a *Citable Authority* for nonhuman animal sentience and cognition: a policy-relevant scientific bedrock that can be used to significantly influence legal precedent and public policymaking in service of animal protection. This information can also be utilized in litigation and advocacy for animal well-being, education, and as a practical scientific resource.

The Living Bibliography Project seeks to answer the question, "How do we create an understandable, accessible, and unbiased presentation on the current science of the cognition, sentience, and agency of a specific animal species?" The purpose of this project is to develop and maintain practical and authoritative science-based summaries that any interested person can use to articulate an individual species' attributes of sentience, cognition, and agency—without the need to undertake or commission significant further research. We have commissioned a library of comprehensive reports on strategically chosen high-impact species, to be made readily available to policymakers, advocates, and others for their own uses.

At its simplest level, each Living Bibliography will explore what we know, what we don't know, and what we would still like to know about these animal species.

How to Use this Document

The Brooks Institute has selected a number of "gateway" animal species as subjects for our Living Bibliography library, with an interest in those whose characteristics may be translatable to other species. We refer to these bibliographies as "living" because of our intention to keep the research contained within them current—updated at least annually. Each Living Bibliography will be created and maintained by a panel of experts on that particular species to allow lawyers and advocates to easily represent the species' inherent characteristics using only these materials.

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Introduction

Octopuses, squid, and cuttlefish are remarkable creatures, famed for their intelligence. They are invertebrates—animals without a backbone—and are much more distant from us in evolutionary terms than our fellow mammals, far more distant even than birds, reptiles, and fishes. The last common ancestor of humans and octopuses lived over 560 million years ago. These animals have evolved intelligence by a different path, and their ways of perceiving and interacting with the world are very different from our own. This resource aims to take you inside the minds of octopuses, squid, cuttlefish, and their lesser-known relatives, the nautiluses, using the latest scientific evidence to present an accurate, up-to-date picture of what we know about their capabilities.

Basics

The cephalopod molluscs (often called "cephalopods," a term we will use throughout this resource) are a class of around 750 species, including all species of octopus, squid, cuttlefish, and nautilus. There are two currently existing subclasses of cephalopod: the nautiloids (Nautiloidae), which retain a *hard external shell*; and the coleoids (Coleoidea), *soft-bodied* cephalopods that have internalized or wholly lost the shell, including octopuses, cuttlefish, and squid. All present-day cephalopods are descended from hard-shelled ancestors.

The soft-bodied cephalopods have evolved from a slow-moving ancestor to become fast-moving, voracious predators. They are renowned for their impressive cognitive abilities, many of which are used while hunting. Because of their large brains and cognitive powers, the idea that they might be sentient beings, capable of feeling pain, pleasure, and other emotions, perhaps in their own distinctive forms, has been taken seriously by scientists for a long time. There is continuing uncertainty and debate about these questions, but also a very large amount of relevant evidence, most of it supportive of these ideas.

The cephalopods are separated from humans by at least 560 million years of evolution, and their brains are organized differently from vertebrate brains, and so the forms of cognition and sentience they have evolved are likely to be different from our own. Yet there are also striking parallels and convergences. When we compare the eyes of cephalopods to vertebrate eyes, we find an uncanny blend of convergently evolved similarities and striking differences, and the same is true of their mental capacities.

This annotated living bibliography provides a comprehensive overview of the peer-reviewed scientific evidence on questions of cognition and sentience. It is organized into 11 categories, introduced below.

Diversity of the Cephalopods

The cephalopods are a hugely diverse group of marine invertebrates. They are well known for fast movement, highly articulate arms and tentacles, rapid color-changing abilities, and advanced brains. These traits have enabled cephalopods to thrive in a broad range of habitats across the world's marine ecosystems, from the deep sea and polar regions to shallow coastal environments and tropical reefs. We see immense variation in the forms and strategies cephalopods have evolved to meet the challenges of their environments. Read the full entry on diversity of the cephalopods.

Perceiving the World

Cephalopods perceive the world by sensing light, contact, and chemicals in the environment. Whereas our eyes are sensitive to the wavelength of the light (leading to color vision), cephalopod eyes are sensitive to the orientation of the light, its polarization. They are very sensitive to pressure changes, allowing them to register sound waves despite lacking ears. The suckers on their arms are richly covered in chemosensing receptors, allowing them to “taste” the environment through contact. Read the full entry on perceiving the world.

Problem-Solving and Intelligence

Octopuses and cuttlefish, in particular, have earned their reputation for intelligence through a mixture of laboratory experiments and behaviors observed in the wild. Octopuses can manipulate their physical environment very skillfully, lifting up cylinders to access the prey within, and even unscrewing jars. They have many techniques for opening up bivalves and will select the most appropriate technique for the task at hand. Read the full entry on problem-solving and intelligence.

Learning and Memory

Given their reputation for intelligence, it can be a surprise to learn that cephalopods have quite short lifespans (for example, cuttlefish usually live around 1–2 years). Yet they learn a huge amount about the world around them in this time, and they use various different mechanisms to do it. They are proficient at many forms of associative learning, a broad type of learning in which connections between sensory stimuli, actions, and outcomes are learned. Cuttlefish also have advanced types of learning and memory once thought to be unique to large-brained vertebrates. For example, it seems they can remember the details of specific past events. Read the full entry on learning and memory.

Sociality and Mating Strategies

On the whole, cephalopods are not particularly social animals outside of the context of reproduction. However, their mating behaviors are complex and often require rapid decisions, subtle forms of communication (sometimes through skin color patterns), and the ability to remember past mates. Read the full entry on sociality and mating strategies.

Navigating the Environment

The soft-bodied cephalopods have a suite of adaptations that allow them to hunt prey with ruthless effectiveness—and to find safety before falling prey themselves to other predators. To achieve this, they use a variety of efficient strategies, taking full advantage of their advanced sensory abilities and an impressive capacity for learning and thinking about the spatial environment. To survive, they must locate and remember food sources, find their way back to shelter or home territories after tracing out complex foraging routes, and remember the location of other members of their species. Read the full entry on navigating the environment.

Self-Regulation and Self-Awareness

Cuttlefish have displayed remarkable feats of self-control in the form of delayed gratification, refraining from attacking an easy but low-quality prey item (sometimes for over two minutes) because they know a better one will emerge if they wait. The picture regarding self-awareness is a complicated one. Cephalopods clearly have ways of recognizing their arms as their own, but they have not, so far, been found to interact with mirrors in ways that would allow them to pass the famous “mirror-mark” test. Read the full entry on self-regulation and self-awareness.

Emotion

Cephalopods show clear signs of fear and stress when forced to endure unsuitable environments. But what about positive emotions? There is some evidence of “play-like” activities. While such actions might suggest experiences of curiosity or enjoyment, it’s important to acknowledge that our understanding of positive emotions in cephalopods is still at an early stage. Human emotion categories may not do a very good job of describing what is going on. Read the full entry on emotion.

Pain

There is very strong evidence of pain in octopuses, based on experiments that are regarded as standard ways of testing for pain in other animals. There is also substantial evidence in squid and cuttlefish. There is very little evidence one way or the other concerning nautiluses. Yet to err on the side of caution, we should assume that all cephalopods—not just octopuses—are capable of experiencing pain. Read the full entry on pain.

Key Welfare Needs

Caring for any cephalopod species requires a deep understanding of that species’ physiology, ecology, behavior, and cognition. Accumulating evidence in support of sentience in cephalopods have been leading to governmental and scientific initiatives to build better laws, regulations, and guidelines. In 2015, an international team of researchers developed guidelines for the care and welfare of cephalopods in research. This work provided useful recommendations about practices related to the capture, transport, welfare monitoring, anesthesia, euthanasia, and husbandry of cephalopods. Read the full entry on key welfare needs.

Knowledge Gaps

There is much that is still unknown about the cephalopods—and many areas where new evidence would be incredibly valuable. Some major knowledge gaps concern questions such as: Why did cephalopods evolve such high levels of intelligence? What are the brain mechanisms supporting their most impressive behaviors? How are their minds shaped by their sensory abilities? What anesthetics and pain medications work on cephalopods? What positive emotions are they capable of experiencing? How can their nutritional needs be best met when they are kept in captivity? How can they be effectively protected from disease? Read the full entry on knowledge gaps.

Authorship

The text of this resource was written by Jonathan Birch, Peter Morse, Alexandra K. Schnell, and Piero Amodio. The resource may be cited as:

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CHAPTER 1

Diversity of the Cephalopods

The cephalopods (Class: Cephalopoda) are a hugely diverse group of marine invertebrates. Uniquely among molluscs, they have adapted quick forms of locomotion,[1] highly articulate and semi-autonomous arms and tentacles that enable them to grab and manipulate objects,[2] closed circulatory systems that provide efficient oxygen transport and the capacity for higher metabolisms,[3] rapid color-changing abilities that facilitate camouflage and communication,[4] and advanced brains that allow for sophisticated learning and intricate behaviors.[5] Together, these traits have enabled cephalopods to occupy a broad range of ecological niches and habitats across the world's marine ecosystems, from the deep sea and polar regions to shallow coastal environments and tropical reefs.[6],[7],[8]

There are over 800 described species of cephalopods, diverse in size and body plans. For a long time, this diversity—combined with cephalopods' ability to alter their shape, color, and texture—made it very difficult indeed to construct reliable family trees of the relationships among cephalopod species.[9] Fortunately, molecular methods have allowed a much better understanding of the cephalopods' evolutionary history.[9],[10] Modern science recognizes ten extant (that is, currently living) cephalopod orders, related to each other in the way depicted in Figure 1.

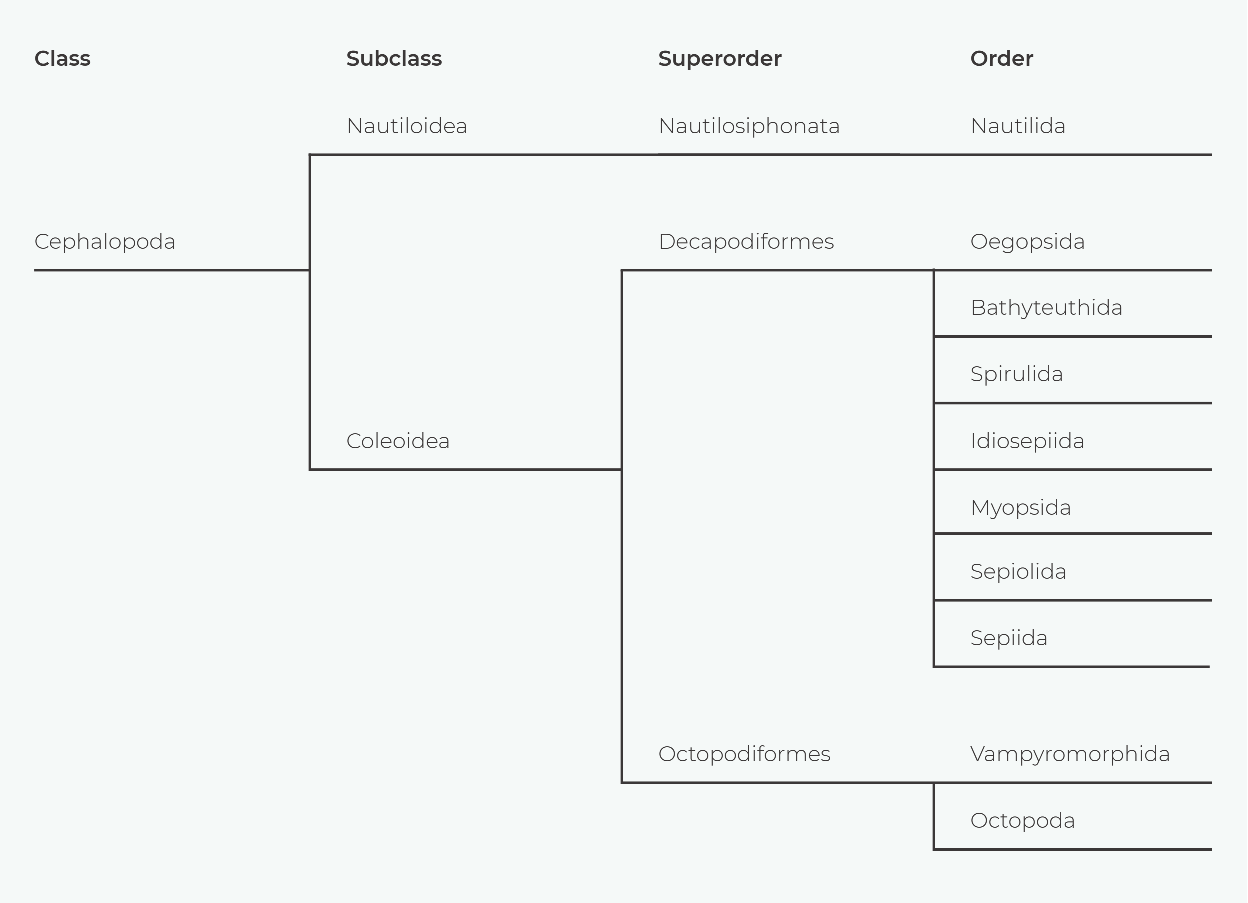

FIGURE 1. The evolutionary relationships of the ten living cephalopod orders. Branch lengths are not to scale (i.e. they do not represent evolutionary time).

The Nautiloids

The *nautiloids* are the oldest cephalopod lineage, and the only group to retain the ancestral trait of possessing an external shell.[11] They first appeared in the fossil record during the upper Cambrian period (approximately 500 million years ago).[12] There were once many more species than now exist. Modern nautiloids are only represented by nine currently described species.[6],[13] The living nautiloids belong to the order Nautilida and are informally called *nautilids*.

Nautilids are different to all other living cephalopods in their morphology, life history, and behavior. Living nautilids have a coiled, chambered external shell that helps them with

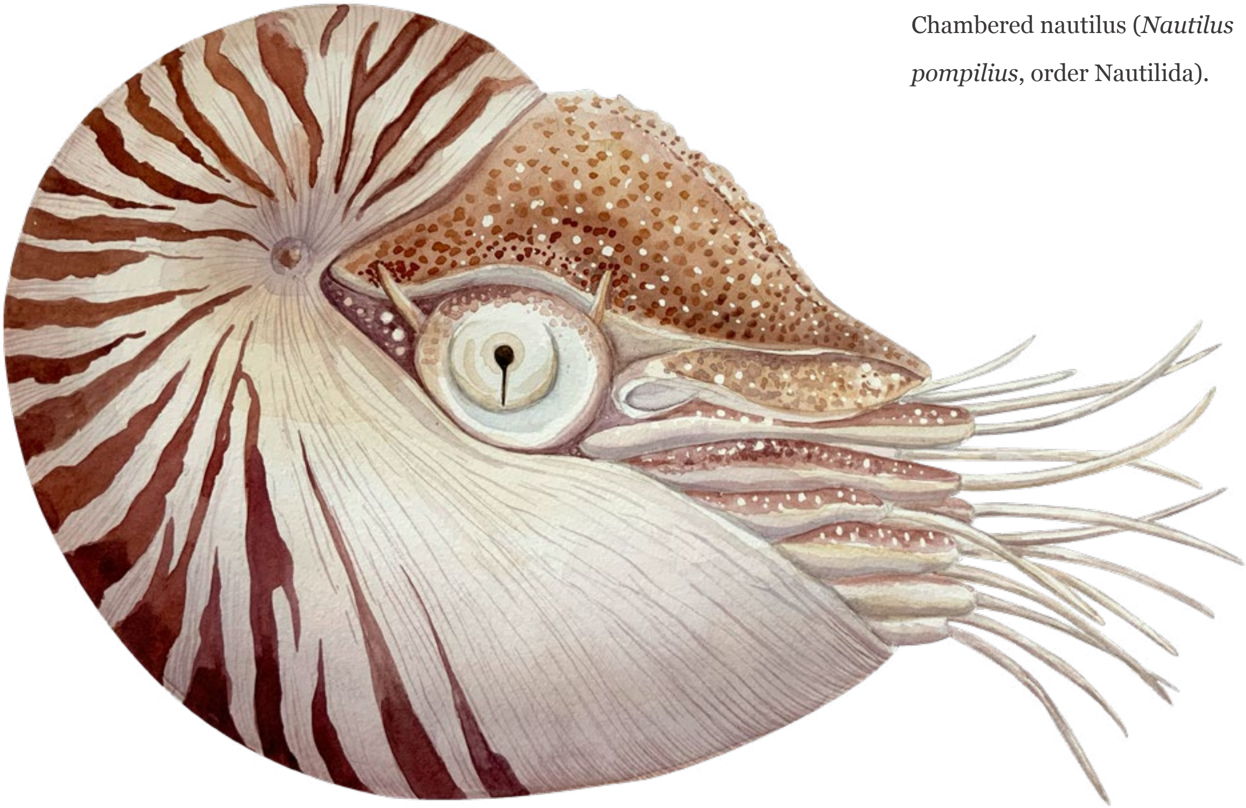

FIGURE 2.

Chambered nautilus (*Nautilus pompilius*, order Nautilida).

buoyancy regulation and protection against predators. They also have more than 90 tentacles that they use for feeding and mating[11] (Figure 2). In the wild, they live in the "coral triangle" region of the Indian and Pacific Oceans. They can live to depths of 700 m or more, and often migrate to shallower waters nocturnally to forage and hunt for food.[14] Nautilids can live for more than twenty years and have been observed to breed annually once mature.[15]

The Coleoids

Most currently living cephalopod species are *coleoid*, or soft-bodied, cephalopods. The coleoids have internalized and reduced—or completely lost—the ancestral shell. In doing this, coleioid cephalopods have become faster and more flexible[1] but have needed to rely on specialized behavioral strategies to avoid predation.[2]

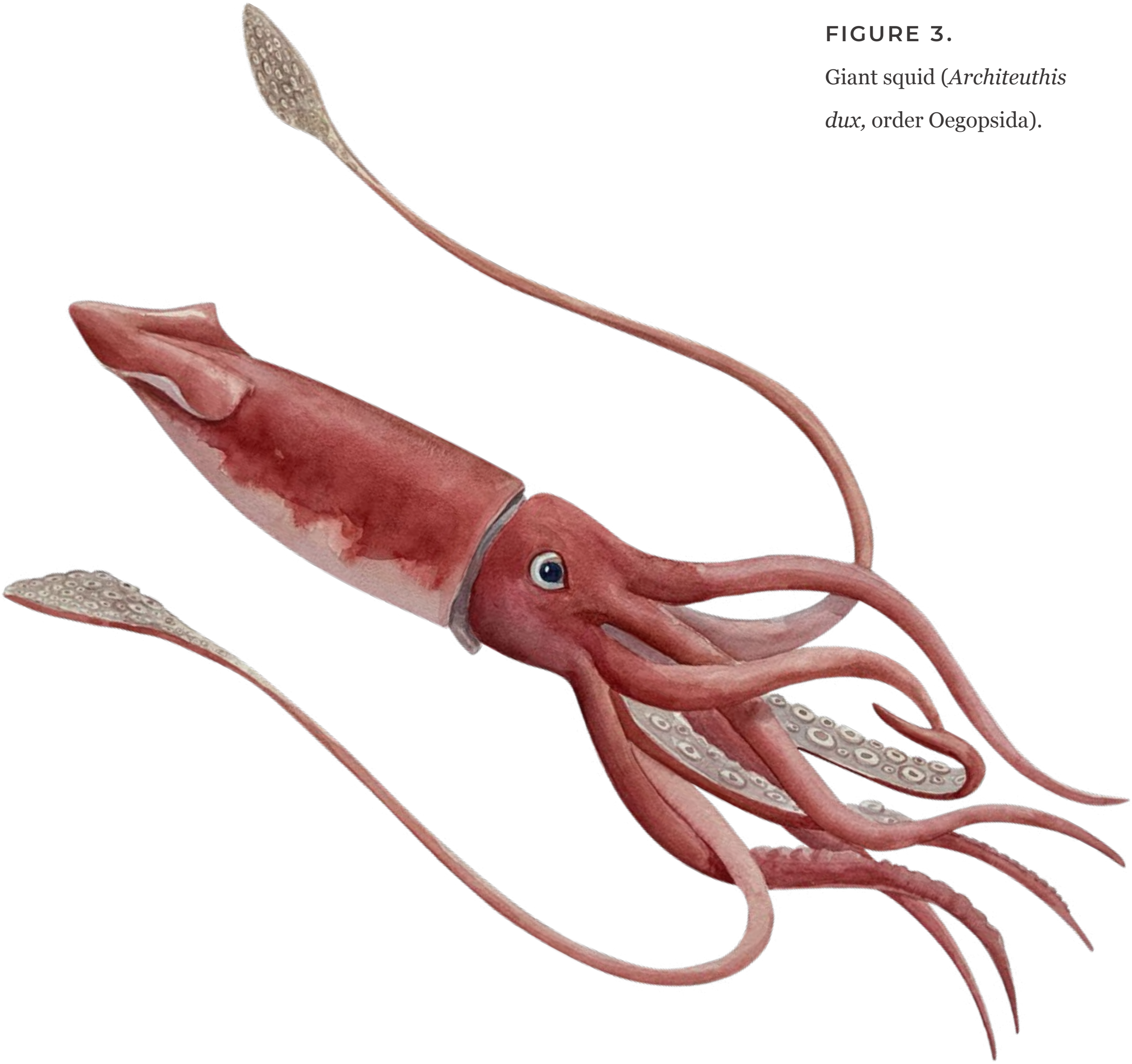

FIGURE 3.

Giant squid (*Architeuthis dux,* order Oegopsida).

OPEN-EYE SQUIDS

The oegopsids, or open-eye squids, are a large order containing at least 230 species.[9] As the common name suggests, oegopsids lack corneal coverings over their eyes. Further traits that distinguish them from other squids are paired female oviducts, a lack of tentacle pockets, and, in many species, the presence of hooks on their arm and tentacle clubs.[7] Oegopsids range across the all ocean basins.[7] This order contains the two largest cephalopods in the world, the giant squid (*Architeuthis dux*: around 13 m total length, Figure 3) and colossal squid (*Mesonychoteuthis hamiltoni*: around 14 m total length).

FIGURE 4.

Deep-sea squid (*Bathyteuthis berryi*, order Bathyteuthida).

DEEP-SEA SQUIDS

The bathyteuthids, or deep-sea squids, are similar to the oegopsids in overall appearance but possess tentacle pockets[16] (Figure 4). All described species live deep in the sea, between 200 m and 4,000 m depth.[7] Due to their habitat, observations of these squid in the wild are rare. However, maternal care in the form of brooding an egg-sheet in mid-water has been observed for one species, *Bathyteuthis berryi*.[17]

THE RAM'S HORN SQUID

Spirulida is an order containing just one species, *Spirula spirula*, otherwise known as the ram's horn squid for its spiral-shaped internal shell, which it uses for regulating buoyancy (Figure 5). This small squid (up to 45 mm) inhabits deep waters (100–1,750 m) along tropical and subtropical continental shelves and oceanic islands.[6] *Spirula spirula* are thought to live between 18 and 20 months, and it has been suggested that females might lay eggs at the bottom of continental slopes.[6] This species also has a green photophore, or light-emitting organ, at the tip of the mantle, which offers camouflage from predators by a method called "counter-illumination"—producing light to cancel out one's shadow when viewed from below.[18]

PYGMY SQUIDS

The idiosepiids, or pygmy squids, are the world's smallest cephalopods, reaching a maximum of only 21 mm in mantle length[6] (Figure 6). There are currently eight described species.[19] They live within shallow-water, coastal environments within the Indo-west Pacific.[6] Idiosepiids typically live in seagrass and mangrove habitats, where they use an oval adhesive organ to adhere to blades of seagrass or seaweed.[20] Depending on species, idiosepiids live for only 80–150 days, and spawn continuously once mature.[21]

CLOSED-EYE SQUIDS

The myopsids, or closed-eye squids, are a relatively well-studied and commercially important order of squids, due to their worldwide distribution across coastal waters.[7] There are approximately fifty species, and they differ from other squid groups principally in that they have a transparent corneal

FIGURE 5.

Above, ram's horn squid (*Spirula spirula*, order Spirulida).

FIGURE 6.

Below, tropical pygmy squid (*Idiosepius pygmaeus*, order Idiosepiida).

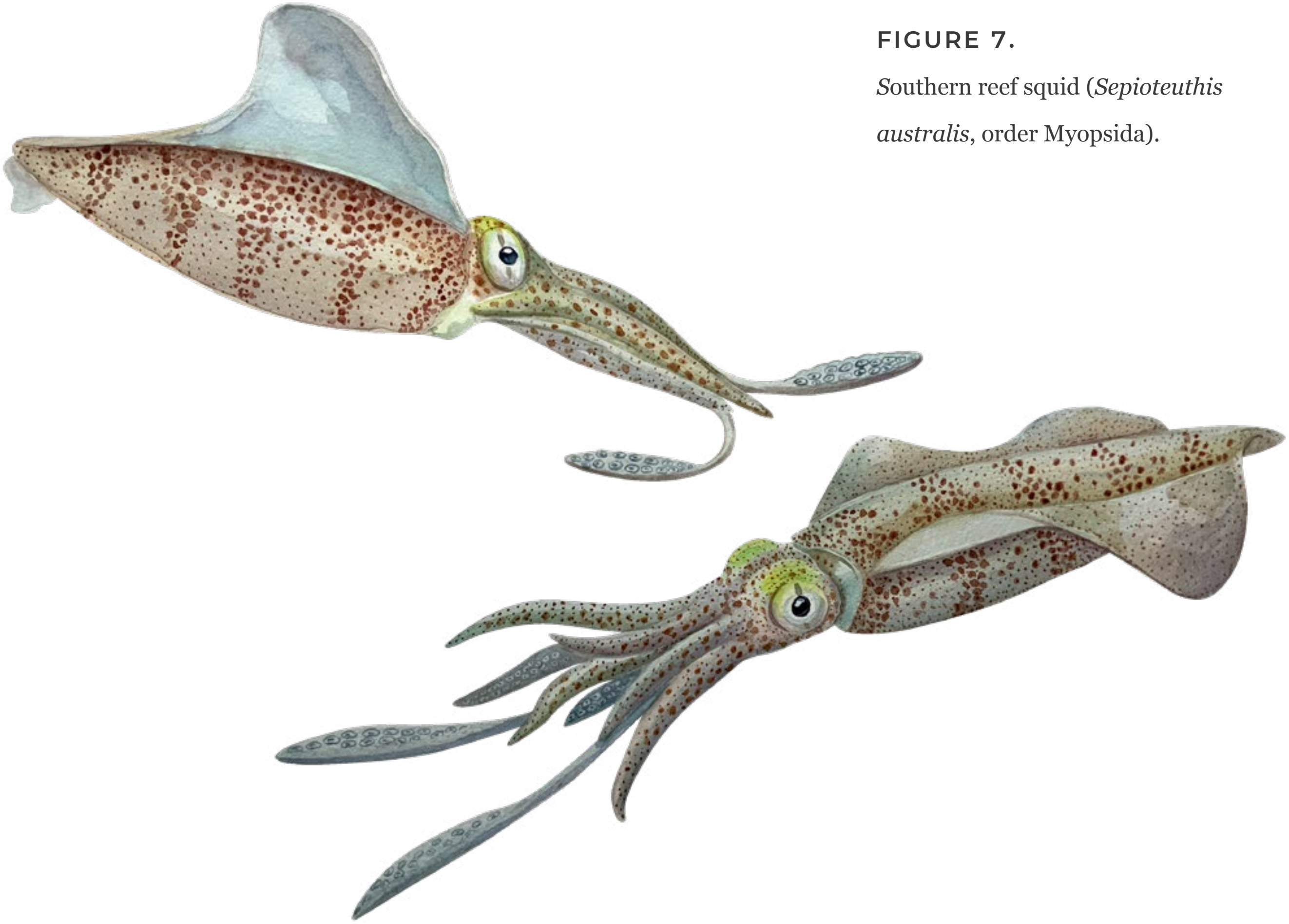

FIGURE 7.

Southern reef squid (*Sepioteuthis australis*, order Myopsida).

membrane over their eyes. They possess tentacle pockets and their suckers lack hooks[7] (Figure 7). The largest myopsid, *Loligo forbesii*, can reach a length of 937 mm.[7] They are considered the most social of the cephalopod orders, since all myopsids hunt and breed in shoals.[22] Depending on the species, myopsids will live for one to two years[23] and die after a single breeding season.[24]

DUMPLING SQUIDS

The sepiolids, or dumpling squids, are a group of small (10–80 mm mantle length) round-shaped squids lacking any form of bone or internalized shell.[6] There are currently 73 described species of sepiolid, split among the two families: Sepiolidae (Figure 8), or bobtail squid; and Sepiadariidae (Figure 9), or bottletail squid.[25] There is currently some debate around whether the sepiolids should be a suborder (Sepiolina) within the larger Sepiida order.[26]

Sepiolids are found across all oceans.[25] Each of the sepiolid families has unique anti-predator strategies. The bobtail squids use symbiosis with bacterial species to create counter-illumination camouflage, and in some cases they distract predators by discharging luminous secretions.[27],[28] The bottletail squids are able to secrete a toxic slime to ward off predators.[29] In recent years, several members of the Sepiolida have become model organisms for cephalopod research, owing to their simple culture and husbandry requirements under laboratory conditions.[30],[25]

CUTTLEFISH

The sepiids, or cuttlefish, are a group of approximately 120 species ranging across the world's tropical and temperate coastal regions except for the Americas[6] (Figure 10). Cuttlefish are known for their unique internalized shell, or cuttlebone, that they use for buoyancy regulation.[6] Most cuttlefish species live up to two years and spawn intermittently.[31],[32]

Due to their unique anatomy, behavior, commercial importance, and coastal

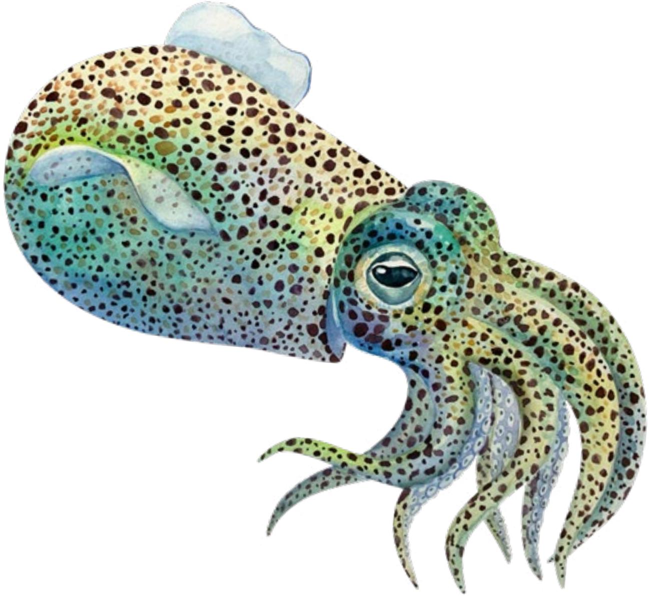

FIGURE 8.

Above, southern bobtail squid (*Euprymna tasmanica*; order Sepiolida, Sepiolidae family).

FIGURE 9.

Below, striped pyjama squid (*Sepioloidea lineolata*; order Sepiolida, Sepidariidae family).

FIGURE 10.

Australian giant cuttlefish (*Sepia apama*, order Sepiida).

abundance, cuttlefish have been the model species for a vast amount of cephalopod research. Much of this research has been focused on their advanced visual systems,[33] camouflage,[34] communication,[35] learning,[36] memory,[37] and reproductive behaviors.[38] Cuttlefish have consistently astounded researchers with their apparently sophisticated levels of cognition and the complexity of their behavior.

THE VAMPIRE SQUID

The order Vampyromorphida contains a single living species, the vampire squid (*Vampyroteuthis infernalis*, Figure 11). As shown in Figure 1, this species is thought to be closer in evolutionary terms to the octopods (*below*) than to the other squids (*above*). The vampire squid has two long retractable filaments between the first two pairs of arms that are used in feeding.[39] These filaments are similar in nature to the feeding tentacles of other squids but have different evolutionary origins.[40]

Vampire squid are found at depths of 500–3,000 m within tropical to subtropical regions.[8] Their eight arms are connected by a dark webbing, and their arms are lined with fleshy, spine-like cirri.

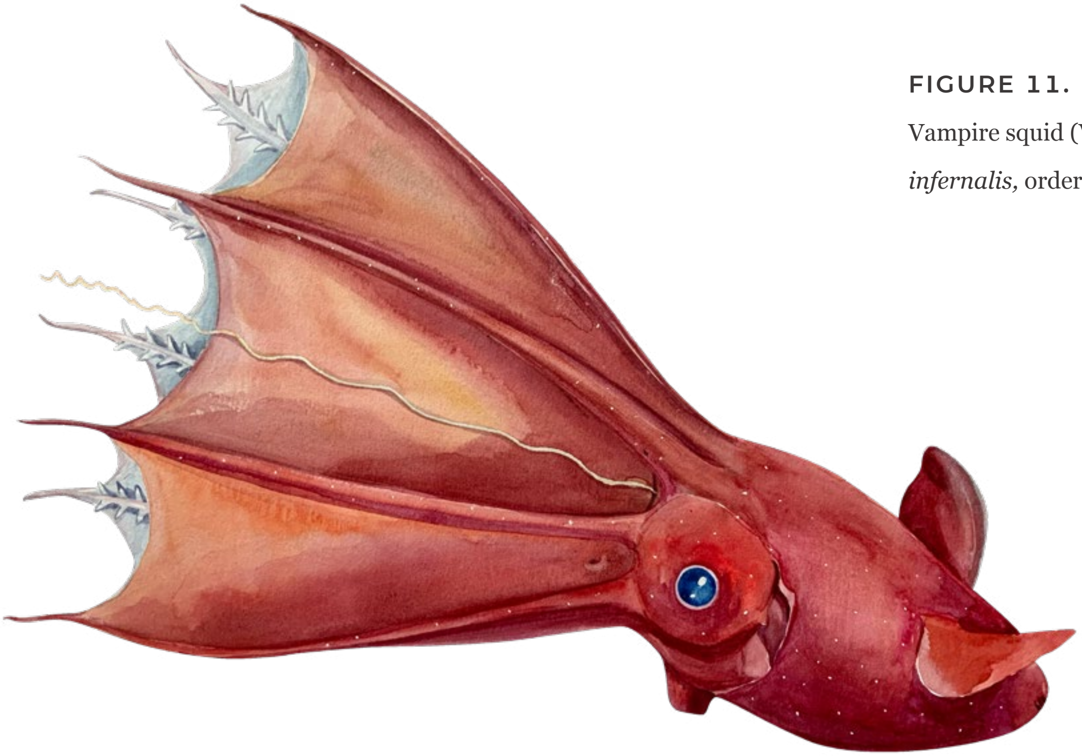

FIGURE 11.

Vampire squid (V*ampyroteuthis infernalis,* order Vampyroteuthida).

Adult vampire squids have lateral fins on either side of the mantle to aid in swimming.[41] They are covered almost entirely in light-emitting photophores[42] and can produce a viscous, luminous fluid from their arm tips.[43] These light-tricks are thought to help vampire squids disorient and escape from potential deep-sea predators.[43] Due to the inaccessibility of their habitats, sightings are rare, and much of what we know of vampire squids' biology is limited to observations made from dead specimens.

OCTOPODS

Octopods are the largest cephalopod order, represented by more than 300 described species.[9] They can be further categorized into two suborders: the Cirrata (Figure 12), or deep-sea cirrate octopods; and the Incirrata (Figure 13), or incirrate octopods, which are better studied.

Cirrate octopods are named for the pairs of cirri that line each of their suckers. They are easily differentiated from incirrate octopods by their paired swimming fins on either side of the mantle. These muscular fins are supported by a well-developed, cartilage-like internal shell, absent in other Octopodiformes.[44] Cirrate octopods typically live at depths greater than 300 m but can live in shallower waters closer to the polar regions.[45]

Incirrate octopods are found across the globe[8] and are subdivided further into two superfamilies. Members of the superfamily Argonautoidea have a unique reproductive trait in which males remove a specialized mating arm to offer to females for sperm transfer during mating.[46] The other superfamily, Octopodoidea, contains the famed shallow-water, coastal species of the Octopodidae family (octopuses)[47] that have been the focus of much cephalopod research.

Octopuses have fast-growth rates,[48] short life-cycles,[49] and in most cases breed once and then die.[24] They combine these traits with elaborate hunting strategies[50] and noted capacities for problem solving[51] and memory[52] (see "Problem Solving and Intelligence," "Learning and Memory"). Like the cuttlefish, they feature heavily in other parts of this guide.

FIGURE 12.

Flapjack octopus (*Opisthoteuthis agassizii*; order Octopoda, suborder Cirrata).

FIGURE 13.

Common octopus (*Octopus vulgaris*; order Octopoda, suborder Incirrata)

CONCLUSION

Despite the rich biodiversity of cephalopod taxa, the majority of cephalopod research has been limited to shallow-water, coastal species that are active in daylight. This bias in research towards more accessible species has constrained our knowledge of cephalopod biology and behavior to only a small subset of cephalopod species, concentrated within about half of the cephalopod orders. Current understanding of behavior or cognition is extremely lacking for deep-sea cephalopods. Whenever they are studied, cephalopods have captivated and astonished their observers with unique behavioral adaptations—strategies that have enabled this class of invertebrates to flourish and radiate across the world’s oceans.

References

1 a b Alupay and Mather 2017

2 a b Amodio et al. 2018

3 Reiber and McGaw 2009

4 Mäthger and Hanlon 2007

5 Shigeno et al. 2018

6 a b c d e f g h i Jereb and Roper 2005

7 a b c d e f g Jereb and Roper 2010

8 a b c Jereb et al. 2014

9 a b c d Allcock et al. 2015

10 Sanchez et al. 2018

11 a b Saunders and Landman 2010

12 Mutvei et al. 2007

13 Barord et al. 2023

14 Dunstan et al. 2011b

15 Dunstan et al. 2011a

16 Young et al. 2019

17 Bush et al. 2012

18 Lindsay et al. 2020

19 Reid et al. 2023

20 Kasugai 2000

21 Nishiguchi et al. 2014

22 Ikeda 2009

23 Jackson 2004

24 a b Rocha et al. 2001

25 a b c Sanchez et al. 2021

26 Ponder et al. 2020

27 Dilly and Herring 1978

28 Boettcher et al. 1996

29 Caruana et al. 2019

30 Squires et al. 2013

31 Gabr et al. 1998

32 Laptikhovsky et al. 2003

33 Temple et al. 2012

34 Chiao and Hanlon 2001

35 Schnell et al. 2016

36 Dickel et al. 2000

37 Schnell et al. 2021

38 Schnell et al. 2015

39 Hoving and Robison 2012

40 Pickford 1949

41 Seibel et al. 1998

42 Herring et al. 1994

43 a b Robison et al. 2003

44 Vecchione and Young 1997

45 Collins and Villanueva 2006

46 Strugnell et al. 2014

47 Freitas et al. 2022

48 Batista et al. 2021

49 Boyle 1983–1987

50 Bayley and Rose 2020

51 Fiorito et al. 1990

52 Hochner et al. 2006

Key Texts

Allcock, A. Louise, A. Lindgren, and Jan M. Strugnell. 2015. “The Contribution of Molecular Data to Our Understanding of Cephalopod Evolution and Systematics: A Review.” In “Cephalopod International Advisory Council Symposium 2012: Interdisciplinary Approaches to Cephalopod Biology.” Special issue, *Journal of Natural History* 49 (21–24): 1373–1421. https://doi.org/10.1080/00222933.2013.825342.

This is an excellent resource for understanding the higher level relationships among the different cephalopod clades, based on recent innovations using molecular markers.

Jereb, Patrizia, and Clyde F. E. Roper, eds. 2005. *Chambered Nautiluses and Sepioids*. Vol. 1 of C*ephalopods of the World: An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date*. FAO Species Catalogue for Fishery Purposes, no. 4, vol. 1. FAO. https://openknowledge.fao.org/handle/20.500.14283/a0150e.

This is a comprehensive field guide, highlighting the life histories, distributions, and defining features for cephalopod taxa within the Nautilida, Spurilida, Idiosepiida, Sepiolida, and Sepiida orders.

Jereb, Patrizia, and Clyde F. E. Roper, eds. 2010. *Myopsid and Oegopsid Squids*. Vol. 2 of C*ephalopods of the World: An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date*. FAO Species Catalogue for Fishery Purposes, no. 4, vol. 2. FAO. https://openknowledge.fao.org/handle/20.500.14283/i1920e.

This is a comprehensive field guide, highlighting the life histories, distributions, and defining features for cephalopod taxa within the Oegopsida, Bathyteuthida, and Myopsida orders.

Jereb, Patrizia, Clyde F. E. Roper, Mark D. Norman, and Julian K. Finn, eds. 2014. *Octopods and Vampire Squids*. Vol. 3 of *Cephalopods of the World: An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date*. Species Catalogue for Fishery Purposes, no. 4, vol. 3. FAO. https://openknowledge.fao.org/handle/20.500.14283/i3489e.

This is a comprehensive field guide, highlighting the life histories, distributions, and defining features for cephalopod taxa within the Vampyroteuthida and Octopoda orders.

Rocha, Francisco, Ángel Guerra, and Ángel F. González. 2001. “A Review of Reproductive Strategies in Cephalopods.” *Biological Reviews* 76 (3): 291–304. https://doi.org/10.1017/S1464793101005681.

This useful review synthesizes and defines the different reproductve strategies present among the various cephalopod clades.

Sanchez, Gustavo, Fernando Á. Fernández-Álvarez, Morag Taite, et al. 2021. “Phylogenomics Illuminates the Evolution of Bobtail and Bottletail Squid (Order Sepiolida).” *Communications Biology* 4:819. https://doi.org/10.1038/s42003-021-02348-y.

This excellent molecular study clarifies the evolutionary relationships within the enigmatic clade Sepiolida.

Sanchez, Gustavo, Davin H. E. Setiamarga, Surangkana Tuanapaya, et al. 2018. “Genus-Level Phylogeny of Cephalopods Using Molecular Markers: Current Status and Problematic Areas.” *PeerJ* 6:e4331. https://doi.org/10.7717/peerj.4331.

This is a comprehensive study, resolving genus-level relationships among the coleoid cephalopods, using a variety of molecular methods.

Saunders, W. Bruce, and Neil H. Landman, eds. 2010. *Nautilus: The Biology and Paleobiology of a Living Fossil*. Topics in Geobiology, vol 6. Springer.

This is the “go to” textbook for any information on the life history and biology of the living Nautilida taxa.

Strugnell, Jan M., Mark D. Norman, Michael Vecchione, Michelle Guzik, and A. Louise Allcock. 2014. “The Ink Sac Clouds Octopod Evolutionary History.” In “Cephalopod Life History, Ecology and Evolution,” edited by Erica A. G. Vidal, Michael Vecchione, and Sigurd von Boletzky. Special issue, *Hydrobiologia* 725 (March): 215–235. https://doi.org/10.1007/s10750-013-1517-6.

This molecular study resolves and defines the evolutionary history of the different clades within the Octopoda order.

Bibliography

Allcock, A. Louise, A. Lindgren, and Jan M. Strugnell. 2015. "The Contribution of Molecular Data to Our Understanding of Cephalopod Evolution and Systematics: A Review." In "Cephalopod International Advisory Council Symposium 2012: Interdisciplinary Approaches to Cephalopod Biology." Special issue, *Journal of Natural History* 49 (21–24): 1373–1421. https://doi.org/10.1080/00222933.2013.825342.

Alupay, Jean, and Jennifer A. Mather. 2017. "Locomotion of Coleoid Cephalopods." In *Physiology of Molluscs: A Collection of Selected Reviews*, vol. 1, edited by Saber Saleuddin and Spencer Mukai. Apple Academic Press.

Amodio, Piero, Markus Boeckle, Alexandra K. Schnell, Ljerka Ostojíc, Graziano Fiorito, and Nicola S. Clayton. 2019. "Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence?" *Trends in Ecology and Evolution* 34 (1): 45–56. https://doi.org/10.1016/j.tree.2018.10.010.

Arnold, John M. (1987) 2010. "Reproduction and Embryology of Nautilus." In *Nautilus: The Biology and Paleobiology of a Living Fossil*, edited by W. Bruce Saunders and Neil H. Landman. Topics in Geobiology, vol 6. Springer.

Gregory J. Barord, David J. Combosch, Gonzalo Giribet, et al. 2023. "Three New Species of *Nautilus* Linnaeus, 1758 (Mollusca, Cephalopoda) from the Coral Sea and South Pacific." *ZooKeys* 1143:51–69. https://doi.org/10.3897/zookeys.1143.84427.

Batista, B. B., H. Matthews-Cascon, R. Marinho, E. Kikuchi, and Manuel Haimovici. 2021. "The Growth and Population Dynamics of *Octopus insularis* Targeted by a Pot Longline Fishery in North-Eastern Brazil." *Journal of the Marine Biological Association of the United Kingdom* 101 (6): 935–946. https://doi.org/10.1017/S0025315421000898.

Bayley, D. T. I., and A. Rose. 2020. "Multi-Species Co-Operative Hunting Behaviour in a Remote Indian Ocean Reef System." *Marine and Freshwater Behaviour and Physiology* 53 (1): 35–42. https://doi.org/10.1080/10236244.2020.1746658.

Boettcher, K., E. Ruby, and M. McFall-Ngai. 1996. "Bioluminescence in the Symbiotic Squid *Euprymna scolopes* Is Controlled by a Daily Biological Rhythm." *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 179 (1): 65–73. https://doi.org/10.1007/BF00193435.

Boyle, P. R., ed. 1983–1987. *Cephalopod Life Cycles*. 2 vols. Academic Press.

Bush, Stephanie L., Hendrik J. T. Hoving, Christine L. Huffard, Bruce H. Robison, and Louis D. Zeidberg. 2012. "Brooding and Sperm Storage by the Deep-Sea Squid *Bathyteuthis berryi* (Cephalopoda: Decapodiformes)." *Journal of the Marine Biological Association of the United Kingdom* 92 (7): 1629–1636. https://doi.org/10.1017/S0025315411002165.

Caruana, Nikeisha J., Jan M. Strugnell, Pierre Faou, Julian Finn, and Ira R. Cooke. 2019. "Comparative Proteomic Analysis of Slime from the Striped Pyjama Squid, *Sepioloidea lineolata*, and the Southern Bottletail Squid, *Sepiadarium austrinum* (Cephalopoda: Sepiadariidae)." *Journal of Proteome Research* 18 (3): 890–899. https://doi.org/10.1021/acs.jproteome.8b00569.

Chiao, Chuan-Chin, and Roger T. Hanlon. 2001. "Cuttlefish Camouflage: Visual Perception of Size, Contrast and Number of White Squares on Artificial Checkerboard Substrata Initiates Disruptive Coloration." *Journal of Experimental Biology* 204 (12): 2119–2125. https://doi.org/10.1242/jeb.204.12.2119.

Collins, Martin A., and Roger Villanueva. 2006. "Taxonomy, Ecology and Behaviour of the Cirrate Octopods." In *Oceanography and Marine Biology: An Annual Review*, vol. 44, edited by R. N. Gibson, R. J. A. Atkinson, and J. D. M. Gordon. CRC Press.

Dickel, Ludovic, Jean Geary Boal, and Bernd U. Budelmann. 2000. "The Effect of Early Experience on Learning and Memory in Cuttlefish." *Developmental Psychobiology* 36 (2): 101–110. https://doi.org/10.1002/(SICI)1098-2302(200003)36:2%3C101::AID-DEV2%3E3.0.CO;2-L.

Dilly, P. N., and P. J. Herring. 1978. "The Light Organ and Ink Sac of *Heteroteuthis dispar* (Mollusca: Cephalopoda)." *Journal of Zoology* 186 (1): 47–59. https://doi.org/10.1111/j.1469-7998.1978.tb03356.x.

Dunstan, Andrew J., Peter D. Ward, and N. Justin Marshall. 2011a "*Nautilus pompilius* Life History and Demographics at the Osprey Reef Seamount, Coral Sea, Australia." *PLOS ONE* 6 (2): e16312. https://doi.org/10.1371/journal.pone.0016312.

Dunstan, Andrew J., Peter D. Ward, and N. Justin Marshall. 2011b. "Vertical Distribution and Migration Patterns of *Nautilus pompilius*." *PLOS ONE* 6 (2): e16311. https://doi.org/10.1371/journal.pone.0016311.

Fiorito, Graziano, Christoph von Planta, and Pietro Scotto. 1990. "Problem Solving Ability of *Octopus vulgaris* Lamarck (Mollusca, Cephalopoda)." *Behavioral and Neural Biology* 53 (2): 217–230. https://doi.org/10.1016/0163-1047(90)90441-8.

Freitas, Yasmim Vieira, Jorge Iván Sánchez-Botero, and Danielle Sequeira Garcez. 2022. "Importância da pesca artesanal para a diversificação proteica e manutenção da segurança alimentar em comunidade litorâneado nordeste do Brasil." *Revista de Arqueología Pública* 17:e022016. https://doi.org/10.20396/rap.v17i00.8668124.

Gabr, Howaida R., Roger T. Hanlon, Mahmoud H. Hanafy, and Salah G. El-Etreby. 1998. "Maturation, Fecundity and Seasonality of Reproduction of Two Commercially Valuable Cuttlefish, *Sepia pharaonis* and *S. dollfusi*, in the Suez Canal." *Fisheries Research* 36 (2–3): 99–115. https://doi.org/10.1016/S0165-7836(98)00107-6.

Herring, P. J., P. N. Dilly, and Celia Cope. 1994. "The Bioluminescent Organs of the Deep-Sea Cephalopod *Vampyroteuthis infernalis* (Cephalopoda: Vampyromorpha)." *Journal of Zoology* 233 (1): 45–55. https://doi.org/10.1111/j.1469-7998.1994.tb05261.x.

Hochner, Binyamin, Tal Shomrat, and Graziano Fiorito. 2006. "The Octopus: A Model for a Comparative Analysis of the Evolution of Learning and Memory Mechanisms." *Biological Bulletin* 210 (3): 308–317. https://doi.org/10.2307/4134567.

Hoving, Hendrik J. T., and Bruce H. Robison. 2012. "Vampire Squid: Detritivores in the Oxygen Minimum Zone." *Proceedings of the Royal Society B: Biological Sciences* 279 (1747): 4559–4567. https://doi.org/10.1098/rspb.2012.1357.

Ikeda, Yuzuru. 2009. "A Perspective on the Study of Cognition and Sociality of Cephalopod Mollusks, a Group of Intelligent Marine Invertebrates." In "Divergence of Comparative Cognitive studies in Japan," edited by Shigeru Watanabe. Special issue, *Japanese Psychological Research* 51 (3): 146–153. https://doi.org/10.1111/j.1468-5884.2009.00401.x.

Jackson, George D. 2004. "Advances in Defining the Life Histories of Myopsid Squid." In "Cephalopod Growth." Special issue, *Marine and Freshwater Research* 55 (4): 357–365. https://doi.org/10.1071/MF03152.

Jereb, Patrizia, and Clyde F. E. Roper, eds. 2005. *Chambered Nautiluses and Sepioids*. Vol. 1 of C*ephalopods of the World: An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date*. FAO Species Catalogue for Fishery Purposes, no. 4, vol. 1. FAO. https://openknowledge.fao.org/handle/20.500.14283/a0150e.

Jereb, Patrizia, and Clyde F. E. Roper, eds. 2010. *Myopsid and Oegopsid Squids*. Vol. 2 of C*ephalopods of the World: An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date*. Species Catalogue for Fishery Purposes, no. 4, vol. 2. FAO. https://openknowledge.fao.org/handle/20.500.14283/i1920e.

Jereb, Patrizia, Clyde F. E. Roper, Mark D. Norman, and Julian K. Finn, eds. 2014. *Octopods and Vampire Squids*. Vol. 3 of *Cephalopods of the World: An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date*. Species Catalogue for Fishery Purposes, no. 4, vol. 3. FAO. https://openknowledge.fao.org/handle/20.500.14283/i3489e.

Kasugai, Takashi. 2000. "Reproductive Behavior of the Pygmy Cuttlefish *Idiosepius paradoxus* in an Aquarium." *Venus: Japanese Journal of Malacology* 59 (1): 37–44. https://doi.org/10.18941/venusjjm.59.1_37.

Laptikhovsky, Vladimir, Alp Salman, Bahadir Önsoy, and Tuncer Katagan. 2003. "Fecundity of the Common Cuttlefish, *Sepia officinalis L.* (Cephalopoda, Sepiida): A New Look at the Old Problem." *Scientia Marina* 67 (3): 279–284. https://doi.org/10.3989/scimar.2003.67n3279.

Lindsay, Dhugal J., James C. Hunt, Mardi McNeil, Robin J. Beaman, and Michael Vecchione. 2020. “The First In Situ Observation of the Ram’s Horn Squid *Spirula spirula* Turns ‘Common Knowledge’ Upside Down.” *Diversity* 12 (12): 449. https://doi.org/10.3390/d12120449.

Mäthger, Lydia M., and Roger T. Hanlon. 2007. “Malleable Skin Coloration in Cephalopods: Selective Reflectance, Transmission and Absorbance of Light by Chromatophores and Iridophores.” *Cell and Tissue Research* 329 (1): 179–186. https://doi.org/10.1007/s00441-007-0384-8.

Morse, Peter, and Christine L. Huffard. 2019. “Tactical Tentacles: New Insights on the Processes of Sexual Selection Among the Cephalopoda.” *Frontiers in Physiology* 10:1035. https://doi.org/10.3389/fphys.2019.01035.

Mutvei, Harry. 2015. “Characterization of Two New Superorders Nautilosiphonata and Calciosiphonata and a New Order Cyrtocerinida of the Subclass Nautiloidea; Siphuncular Structure in the Ordovician Nautiloid *Bathmoceras* (Cephalopoda).” *GFF* 137 (3): 164–174. https://doi.org/10.1080/11035897.2015.1061592.

Mutvei, Harry, Yun-Bai Zhang, and Elena Dunca. 2007. “Late Cambrian Plectronocerid Nautiloids and Their Role in Cephalopod Evolution.” *Palaeontology* 50 (6): 1327–1333. https://doi.org/10.1111/j.1475-4983.2007.00708.x.

Nishiguchi, M., Jaruwat Nabhitabhata, N. Moltschaniwskyj, and Sigurd von Boletzky. 2014. “A Review of the Pygmy Squid *Idiosepius*: Perspectives Emerging from an ‘Inconspicuous’ Cephalopod.” *Vie et milieu / Life and Environment* 64:23–34.

Pickford, Grace E. 1949. *External Anatomy*. Vol. 2 of *Vampyroteuthis infernalis Chun: An Archaic Dibranchiate Cephalopod*. Dana-Report: The Carlsberg Foundation’s Oceanographical Expedition Round the World 1928–30 and Previous “Dana”-Expeditions 32. Andr. Fred. Høst & Søn.

Ponder, Winston Frank, David R. Lindberg, and Juliet Mary Ponder. 2020. *Biology and Evolution of the Mollusca*, vol. 1. CRC Press.

Reiber, Carl L., and Iain J. McGaw. 2009. “A Review of the ‘Open’ and ‘Closed’ Circulatory Systems: New Terminology for Complex Invertebrate Circulatory Systems in Light of Current Findings.” *International Journal of Zoology*, 2009:301284. https://doi.org/10.1155/2009/301284.

Reid, Amanda, Noriyosi Sato, Jeffrey Jolly, and Jan M. Strugnell. 2023. “Two New Pygmy Squids, *Idiosepius kijimuna* n. sp. and *Kodama jujutsu* n. gen., n. sp. (Cephalopoda: Idiosepiidae) from the Ryukyu Islands, Japan.” *Marine Biology* 170 (12): 167. https://doi.org/10.1007/s00227-023-04305-1.

Robison, Bruce H., Kim R. Reisenbichler, James C. Hunt, and Steven H. D. Haddock. 2003. “Light Production by the Arm Tips of the Deep-Sea Cephalopod *Vampyroteuthis infernalis*.” *Biological Bulletin* 205 (2): 102–109. https://doi.org/10.2307/1543231.

Rocha, Francisco, Ángel Guerra, and Ángel F. González. 2001. “A Review of Reproductive Strategies in Cephalopods.” *Biological Reviews* 76 (3): 291–304. https://doi.org/10.1017/S1464793101005681.

Sanchez, Gustavo, Fernando Á. Fernández-Álvarez, Morag Taite, et al. 2021. “Phylogenomics Illuminates the Evolution of Bobtail and Bottletail Squid (Order Sepiolida).” *Communications Biology* 4:819. https://doi.org/10.1038/s42003-021-02348-y.

Sanchez, Gustavo, Davin H. E. Setiamarga, Surangkana Tuanapaya, et al. 2018. “Genus-Level Phylogeny of Cephalopods Using Molecular Markers: Current Status and Problematic Areas.” *PeerJ* 6:e4331. https://doi.org/10.7717/peerj.4331.

Saunders, W. Bruce, and Neil H. Landman, eds. 2010. *Nautilus: The Biology and Paleobiology of a Living Fossil.* Topics in Geobiology, vol 6. Springer.

Schnell, Alexandra K., Nicola S. Clayton, Roger T. Hanlon, and Christelle Jozet-Alves. 2021. “Episodic-Like Memory Is Preserved with Age in Cuttlefish.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1957): 20211052. https://doi.org/10.1098/rspb.2021.1052.

Schnell, Alexandra K., Carolynn L. Smith, Roger T. Hanlon, Karina C. Hall, and Robert T. Harcourt. 2016. “Cuttlefish Perform Multiple Agonistic Displays to Communicate a Hierarchy of Threats.” *Behavioral Ecology and Sociobiology* 70 (10): 1643–1655. https://doi.org/10.1007/s00265-016-2170-7.

Schnell, Alexandra K., Carolynn L. Smith, Roger T. Hanlon, and Robert T. Harcourt. 2015. “Female Receptivity, Mating History, and Familiarity Influence the Mating Behavior of Cuttlefish.” *Behavioral Ecology and Sociobiology* 69 (2): 283–292. https://doi.org/10.1007/s00265-014-1841-5.

Seibel, Brad A., Erik V. Thuesen, and James J. Childress. 1998. “Flight of the Vampire: Ontogenetic Gait-Transition in *Vampyroteuthis infernalis* (Cephalopoda: Vampyromorpha).” *Journal of Experimental Biology* 201 (16): 2413–2424. https://doi.org/10.1242/jeb.201.16.2413.

Shigeno, Shuichi, Paul L. R. Andrews, Giovanna Ponte, and Graziano Fiorito. 2018. “Cephalopod Brains: An Overview of Current Knowledge to Facilitate Comparison With Vertebrates.” *Frontiers in Physiology* 9:952. https://doi.org/10.3389/fphys.2018.00952.

Squires, Zoe E., Mark D. Norman, and Devi Stuart-Fox. 2013. “Mating Behaviour and General Spawning Patterns of the Southern Dumpling Squid *Euprymna tasmanica* (Sepiolidae): A Laboratory Study.” *Journal of Molluscan Studies* 79 (3): 263–269. https://doi.org/10.1093/mollus/eyt025.

Strugnell, Jan M., Mark D. Norman, Michael Vecchione, Michelle Guzik, and A. Louise Allcock. 2014. "The Ink Sac Clouds Octopod Evolutionary History." In "Cephalopod Life History, Ecology and Evolution," edited by Erica A. G. Vidal, Michael Vecchione, and Sigurd von Boletzky. Special issue, *Hydrobiologia* 725 (March): 215–235. https://doi.org/10.1007/s10750-013-1517-6.

Temple, S. E., V. Pignatelli, T. Cook, et al. 2012. "High-Resolution Polarisation Vision in a Cuttlefish." *Current Biology* 22 (4): R121–R122. https://doi.org/10.1016/j.cub.2012.01.010.

Vecchione, Michael, and Richard E. Young. 1997. "Aspects of the Functional Morphology of Cirrate Octopods: Locomotion and Feeding." *Vie et milieu / Life and Environment* 47 (2): 101–110. https://wwwphp.obs-banyuls.fr/Viemilieu/images/Archives_1950-2002/vie-et-milieu/VOLUME_1997_47_fasc2.pdf.

Young, Richard E., Michael Vecchione, and Katharina M. Mangold. 2019. "Decapodiformes Leach, 1817: Squids, Cuttlefishes and Their Relatives." The Tree of Life Web Project, last modified March 26. http://tolweb.org/Decapodiformes/19404/2019.03.26.

CHAPTER 2

Perceiving the World

Cephalopods possess a range of advanced sensory abilities to perceive the world around them. These abilities help them seek out prey, elude predators, and handle interactions with members of the same species. The sensory systems of cephalopods can be broadly differentiated into the three categories: *photosensory* (sensing light), *mechanosensory* (sensing contact), and *chemosensory* (sensing the chemical environment).[1] The structures involved vary somewhat across different cephalopod species. However, all cephalopods rely on light, together with mechanical and chemical stimulation, to navigate and interact with their surroundings.

Let's start with the *photosensory* (light-sensing) systems. Octopuses, cuttlefish, and squid have advanced "camera-type" eyes that evolved independently of the eyes of vertebrates (a prime example of *convergent evolution*). These include an iris controlling the amount of light entering the pupil, a refractive lens, a vitreous cavity, a layer of photoreceptors forming a retina,[2] and, in octopuses, a fully closed cornea over the lens.[3] These eyes can form perfectly focused images.[4] Unlike human eyes, they have multiple focal points, allowing enhanced perception of moving subjects.[5] This sharp eyesight helps them with hunting,[6] the detection and identification of predators,[7] camouflaging with their environment,[8] visual signaling,[9] and recognition of other members of the same species.[10] By contrast, the nautiloids (cephalopods that retain the hard shell of ancestral forms) have "pinhole" eyes lacking a cornea or refractive lens.[11] They are thought to only perceive very dim, unfocused images.

Most cephalopods are thought unable to differentiate among the different wavelengths of light with their eyes, an ability necessary to perceive colors. This is because they only possess a single type of photoreceptor, in contrast to the various different types, keyed to different wavelengths, found in the eyes of animals that see in color.[12] They have also failed several forms of color discrimination test.[13] The firefly squid (*Watasenia scintillans*) is the only cephalopod known to have three photoreceptor pigments.[14] This may have evolved to help the squid distinguish between ambient light and the bioluminescence of other members of the same species.[15] We cannot entirely rule out something like color vision existing in other cephalopods. It is possible in principle that other cephalopods could distinguish between different wavelengths of light with a single type of photoreceptor, if they use sophisticated enough processing strategies on the information from these photoreceptors.[16]

Cephalopod eyes are sensitive to the polarization of light (roughly, the orientation of the light waves, a property distinct from their wavelength). This polarization-sensitivity is thought to be especially useful in deep-water environments. With increasing depth, light becomes less variable in its wavelength (everything quickly becomes bluish, gradually reducing contrast), whereas contrasts in polarization are unaffected by the depth of the water.[17] Cephalopods probably use this sense for navigation, and for locating fish and crustacean prey items that have highly polarized scales and exoskeletons, respectively.[17] Soft-bodied cephalopods are also capable of changing the polarized patterns of light reflected from their skin.[18] This may provide them with a discreet way of communicating with other members of the same species.[19] While evidence to support this idea is still limited, one female of the species *Octopus djinda* has been reported to display polarized patterns to a male in the laboratory.[20] Cephalopods can also sense light with their *skin*.[21],[22] It is thought that this ability helps them maintain optimal camouflage, as well as ensuring that their bodies are not exposed to visual predators when hiding or resting in a den.[23]

Let’s turn now to the *mechanosensory* (contact-sensing) systems. Cephalopods can feel the texture, movement, and sound of objects around them. A variety of specialized mechanoreceptors are present in the suckers, lining the arms of soft-bodied cephalopods. These are capable of detecting texture and thought to help facilitate the handling of prey, as well as potentially playing a role during mating behavior. The cilia lining the tentacles of nautiloids are thought to serve similar functions.[24] Cuttlefish, squid, and some octopus hatchlings also possess a lateral line system, composed of four or five lines of epidermal hair cells that can detect very slight water movements.[25] They use this for detecting and ambushing prey, and it may also help with predator avoidance and shoaling behavior.

Squid, being active swimmers, have a neck receptor organ that is used for detecting the pitch and roll of the head relative to their bodies.[26] All cephalopods possess organs called statocysts that aid with equilibrium and orientation in the water column by detecting gravity and angular acceleration.[27] There is some evidence that cephalopod statocysts, and potentially their lateral line systems too, are sensitive to sound waves. Various sounds have been observed to elicit startle or escape behavior in cephalopods,[28] despite their lack of ears, leading to the suggestion that cephalopods in the wild might use this ability to evade potential predators.[29] There is also evidence that noise in the environment, caused by humans, can reduce auditory sensitivity in some species.[30]

Finally, let’s turn to the *chemosensory* (chemical-sensing) systems. Nautiloids, which have poor vision, rely heavily on sensing the chemical environment to locate food while scavenging and hunting.[24] Similarly, soft-bodied cephalopods can taste waterborne molecules from a distance using chemoreceptive pits located below their eyes.[31] This helps them to hunt prey,[32] detect predators,[33] and gain valuable information about other animals of the same species.[34] The common cuttlefish (*Sepia officinalis*) has been observed to keep track of the recent mating history of potential partners using distance chemoreception.[35],[36] This is useful for females when choosing a mate, and useful for males when trying to guard a mate. Certain octopus species can discriminate the sex of other members of their species based on chemical signals in the water, and in some cases these same signals have been observed to influence female mate choice.[37]

Cephalopods can "taste" their environment through contact.[38] Nautiloids have contact chemoreceptors on their tentacles, and soft-bodied cephalopods have chemoreceptors on the suckers lining the ventral surfaces of their arms, as well as on the buccal lips (around the mouth) in cuttlefish and squid. Octopuses have approximately 10,000 chemoreceptor cells per sucker, compared to only around 100 chemoreceptors per sucker in cuttlefish and squid.[39],[40] It would seem the way octopuses explore their environment with their arms while foraging for food requires a very high density of chemoreceptors. This ability also aids cephalopods in the acquisition and handling of prey, and, in octopuses, clearly plays a prominent role in how they interact with each other.[41] In the brain of an octopus, the chemosensory lobes, which are responsible for processing chemical stimuli, are integrated with the parts of the brain that regulate signaling in the context of feeding and reproduction.[28] Male blue-ringed octopuses (*Hapalochlaena maculosa*) use chemotactile behavior to identify the sex of other animals of the same species, as well as to determine whether they had already mated or not with a particular female.[42]

Taken together, these impressive sensory abilities allow cephalopods to occupy diverse marine environments, succeed as active marine predators, employ sophisticated predator avoidance strategies and partake in complex reproductive behaviors.[43]

References

1 York 2022

2 Serb and Eernisse 2008

3 Hanke & Kelber 2020

4 Land 1984

5 Talbot and Marshall 2011

6 Budelmann 1996

7 Schnell and Clayton 2019

8 Chiao et al. 2015

9 Boal et al. 2004

10 Tricarico et al. 2011

11 Hurley et al. 1978

12 Chung and Marshall 2016

13 Mäthger et al. 2009

14 Seidou et al. 1990

15 Michinomae et al. 1994

16 Stubbs and Stubbs 2016

17 a b Shashar and Cronin 1996

18 Shashar et al. 1996

19 Mäthger et al. 2006

20 Morse 2008

21 Kingston et al. 2015

22 Ramirez and Oakley 2015

23 Katz et al. 2021

24 a b Ruth et al. 2002

25 Budelmann and Bleckmann 1988

26 Boal et al. 2000

27 Budelmann 1990

28 a b Polese et al. 2015

29 Boal 1996

30 Boal 1997

31 Mollo et al. 2017

32 Preuss and Budelmann 1995

33 Di Cosmo and Polese 2017

34 Samson et al. 2016

35 Wilson et al. 2018

36 Putland et al. 2023

37 Morse et al. 2017

38 van Giesen et al. 2020

39 Graziadei 1964a

40 Graziadei 1964b

41 Morse et al. 2018

42 Morse and Huffard 2022

43 Morse and Huffard 2019

Key Texts

Budelmann, Bernd U. 1996. "Active Marine Predators: The Sensory World of Cephalopods." *Marine and Freshwater Behaviour and Physiology* 27 (2–3): 59–75. https://doi.org/10.1080/10236249609378955.

This comprehensive review compares and contrasts the form and function of sensory systems across the cephalopods.

Di Cosmo, Anna, and Gianluca Polese. 2017. "Cephalopod Olfaction." *Oxford Research Encyclopedia of Neuroscience*, July 27. https://doi.org/10.1093/acrefore/9780190264086.013.185.

This review highlights the importance to cephalopods of taste-like "gustatory systems" involving the skin.

Hanke, Frederike D., and Almut Kelber. 2020. "The Eye of the Common Octopus (*Octopus vulgaris*)." *Frontiers in Physiology* 10:1637. https://doi.org/10.3389/fphys.2019.01637.

This review provides a detailed summary for the form and function of octopus visual systems.

Kingston, Alexandra C. N., Alan M. Kuzirian, Roger T. Hanlon, and Thomas W. Cronin. 2015. "Visual Phototransduction Components in Cephalopod Chromatophores Suggest Dermal Photoreception." *The Journal of Experimental Biology* 218 (10): 1596–1602. https://doi.org/10.1242/jeb.117945.

This research revealed that cephalopods can "see" with their skin.

Mäthger, Lydia M., Nadav Shashar, and Roger T. Hanlon. 2009. "Do Cephalopods Communicate Using Polarized Light Reflections from Their Skin?" *Journal of Experimental Biology* 212 (14): 2133–2140. https://doi.org/10.1242/jeb.020800.

This review of cephalopod visual and dermal systems highlights the capacity for cephalopods to employ a discreet communication strategy using the reflectance of polarized light.

Moody, M. F., and J. R. Parriss. 1961. "The Discrimination of Polarized Light by *Octopus*: A Behavioural and Morphological Study." *Zeitschrift für vergleichende Physiologie* 44 (3): 268–291. https://doi.org/10.1007/BF00298356.

This groundbreaking study revealed that cephalopods are polarization-sensitive. Rather than seeing wavelengths of light, they are sensitive to the orientation of the light.

Morse, Peter, and Christine L. Huffard. 2022. "Chemotactile Social Recognition in the Blue-Ringed Octopus, *Hapalochlaena maculosa*." *Marine Biology* 169 (8): 99. https://doi.org/10.1007/s00227-022-04087-y.

This research provided evidence for the use of "tasting through touch" in octopus social recognition and mating behavior.

Packard, A., Hans Erik Karlsen, and O. Sand. 1990. “Low Frequency Hearing in Cephalopods.” *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 166 (4): 501–505. https://doi.org/10.1007/BF00192020.

This experimental study revealed, that despite lacking specialized hearing organs, species of octopus, cuttlefish, and squid are all sensitive to sound waves.

Polese, Gianluca, Carla Bertapelle, and Anna Di Cosmo. 2015. “Role of Olfaction in *Octopus vulgaris* Reproduction.” *General and Comparative Endocrinology* 210:55–62. https://doi.org/10.1016/j.ygcen.2014.10.006.

This study discovered that the chemosensory lobes of octopuses, which are responsible for processing chemical stimuli, are integrated with the same parts of the brain that regulate signal molecules involved in both feeding and reproductive behaviors. This provides further evidence for the importance of chemical information in cephalopod mating and social behavior.

Ruth, Peter, Henrike Schmidtberg, Bettina Westermann, and Rudolf Schipp. 2002. “The Sensory Epithelium of the Tentacles and the Rhinophore of *Nautilus pompilius* L. (Cephalopoda, Nautiloidea).” *Journal of Morphology* 251 (3): 239–255. https://doi.org/10.1002/jmor.1086.

This detailed study outlines the different organs and specialized cells used for chemosensing in nautiloids.

Walderon, Matthew D., Kevin J. Nolt, Robert E. Haas, et al. 2011. “Distance Chemoreception and the Detection of Conspecifics in *Octopus bimaculoides*.” *Journal of Molluscan Studies* 77 (3): 309–311. https://doi.org/10.1093/mollus/eyr009

This study discovered that some species of octopus can discriminate the sex of other animals of the same species based solely on odor cues in the water. This highlights the importance of chemosensing in cephalopod social behavior.

Bibliography

Amodio, Piero, Markus Boeckle, Alexandra K. Schnell, Ljerka Ostojíc, Graziano Fiorito, and Nicola S. Clayton. 2019. "Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence?" *Trends in Ecology and Evolution* 34 (1): 45–56. https://doi.org/10.1016/j.tree.2018.10.010.

Boal, Jean Geary. 1996. "Absence of Social Recognition in Laboratory-Reared Cuttlefish, *Sepia officinalis* L. (Mollusca: Cephalopoda)." *Animal Behaviour* 52 (3): 529–537. https://doi.org/10.1006/anbe.1996.0195.

Boal, Jean Geary. 1997. "Female Choice of Males in Cuttlefish (Mollusca: Cephalopoda)." *Behaviour* 134 (13–14): 975–988. https://doi.org/10.1163/156853997X00340.

Boal, Jean Geary, and D. K. Golden. 1999. "Distance Chemoreception in the Common Cuttlefish, *Sepia officinalis* (Mollusca, Cephalopoda)." *Journal of Experimental Marine Biology and Ecology* 235 (2): 307–317. https://doi.org/10.1016/S0022-0981(98)00187-7.

Boal, Jean Geary, Nadav Shashar, Melissa Grable, Ellis Loew, Roger T. Hanlon, and Katrina Vaughan. 2004. "Behavioral Evidence for Intraspecific Signaling with Achromatic and Polarized Light by Cuttlefish (Mollusca: Cephalopoda)." *Behaviour* 141 (7): 837–861. https://doi.org/10.1163/1568539042265662.

Boal, Jean Geary, K. M. Wittenberg, and Roger T. Hanlon. 2000. "Observational Learning Does Not Explain Improvement in Predation Tactics by Cuttlefish (Mollusca: Cephalopoda)." *Behavioural Processes* 52 (2–3): 141–153. https://doi.org/10.1016/S0376-6357(00)00137-6.

Budelmann, Bernd U. 1990. "The Statocysts of Squid." In *Squid as Experimental Animals*, edited by Daniel L. Gilbert, William J. Adelman, and John M. Arnold. Springer US.

Budelmann, Bernd U. 1995. "Cephalopod Sense Organs, Nerves and the Brain: Adaptations for High Performance and Life Style." *Marine and Freshwater Behaviour and Physiology* 25 (1–3): 13–33. https://doi.org/10.1080/10236249409378905.

Budelmann, Bernd U. 1996. "Active Marine Predators: The Sensory World of Cephalopods." *Marine and Freshwater Behaviour and Physiology* 27 (2–3): 59–75. https://doi.org/10.1080/10236249609378955.

Budelmann, Bernd U., and Horst Bleckmann. 1988. "A Lateral Line Analogue in Cephalopods: Water Waves Generate Microphonic Potentials in the Epidermal Head Lines of *Sepia* and *Lolliguncula*." *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 164 (1): 1–5. https://doi.org/10.1007/BF00612711.

Budelmann, Bernd U., U. Riese, and Horst Bleckmann. 1991. “Structure, Function, Biological Significance of the Cuttlefish ‘Lateral Lines.’” In *The Cuttlefish: First International Symposium on the Cuttlefish Sepia*, edited by E. Boucard-Camou. Centre de Publications de l’Université de Caen.

Chiao, Chuan-Chin, Charles Chubb, and Roger T. Hanlon. 2015. “A Review of Visual Perception Mechanisms That Regulate Rapid Adaptive Camouflage in Cuttlefish.” In “Invertebrate Neuroscience,” edited by Alison R. Mercer and Bing Zhang. Special issue, *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 201 (9): 933–945. https://doi.org/10.1007/s00359-015-0988-5.

Chung, Wen-Sung, and N. Justin Marshall. 2016. “Comparative Visual Ecology of Cephalopods from Different Habitats.” *Proceedings of the Royal Society B: Biological Sciences* 283 (1838): 20161346. https://doi.org/10.1098/rspb.2016.1346.

Di Cosmo, Anna, and Gianluca Polese. 2017. “Cephalopod Olfaction.” *Oxford Research Encyclopedia of Neuroscience*, July 27. https://doi.org/10.1093/acrefore/9780190264086.013.185.

Graziadei, P. P. C. 1962. “Receptors in the Suckers of *Octopus*.” *Nature* 195 (4836): 57–59. https://doi.org/10.1038/195057a0.

Graziadei, P. P. C. 1964a. “Electron Microscopy of Some Primary Receptors in the Sucker of *Octopus vulgaris.”* *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 64 (4): 510–522. https://doi.org/10.1007/BF01045122.

Graziadei, P. P. C. 1964b. “Receptors in the Sucker of the Cuttlefish.” *Nature* 203 (4943): 384–386. https://doi.org/10.1038/203384a0.

Graziadei, P. P. C., and H. T. Gagne. 1976. “An Unusual Receptor in the Octopus.” *Tissue and Cell* 8 (2): 229–240. https://doi.org/10.1016/0040-8166(76)90049-5.

Hanke, Frederike D., and Almut Kelber. 2020. “The Eye of the Common Octopus (*Octopus vulgaris*).” *Frontiers in Physiology* 10:1637. https://doi.org/10.3389/fphys.2019.01637.

Hawryshyn, C. W. 1992. “Polarization Vision in Fish.” *American Scientist* 80 (2): 164–175. https://www.jstor.org/stable/29774602.

Hurley, Ann C., G. David Lange, and Peter H. Hartline. 1978. “The Adjustable ‘Pinhole Camera’ Eye of *Nautilus*.” *Journal of Experimental Zoology* 205 (1): 37–43. https://doi.org/10.1002/jez.1402050106.

Katz, Itamar, Tal Shomrat, and Nir Nesher. 2021. “Feel the Light: Sight-Independent Negative Phototactic Response in Octopus Arms.” *Journal of Experimental Biology* 224 (5). https://doi.org/10.1242/jeb.237529.

Kingston, Alexandra C. N., Alan M. Kuzirian, Roger T. Hanlon, and Thomas W. Cronin. 2015. "Visual Phototransduction Components in Cephalopod Chromatophores Suggest Dermal Photoreception." *The Journal of Experimental Biology* 218 (10): 1596–1602. https://doi.org/10.1242/jeb.117945.

Land, M. F. 1984. "Molluscs." In *Photoreception and Vision in Invertebrates*, edited by M. A. Ali. NATO Science Series A: Life Sciences 74. Springer.

Mäthger, Lydia M., Alexandra Barbosa, Simon Miner, and Roger T. Hanlon. 2006. "Color Blindness and Contrast Perception in Cuttlefish (*Sepia officinalis*) Determined by a Visual Sensorimotor Assay." *Vision Research* 46 (11): 1746–1753. https://doi.org/10.1016/j.visres.2005.09.035.

Mäthger, Lydia M., Nadav Shashar, and Roger T. Hanlon. 2009. "Do Cephalopods Communicate Using Polarized Light Reflections from Their Skin?" *Journal of Experimental Biology* 212 (14): 2133–2140. https://doi.org/10.1242/jeb.020800.

Messenger, John B. 1977. "Evidence That *Octopus* Is Colour Blind." *Journal of Experimental Biology* 70 (1): 49–55. https://doi.org/10.1242/jeb.70.1.49.

Michinomae, Masanao, Hiroko Masuda, Masatsugu Seidou, and Yuji Kito. 1994. "Structural Basis for Wavelength Discrimination in the Banked Retina of the Firefly Squid *Watasenia scintillans*." *Journal of Experimental Biology* 193 (1): 1–12. https://doi.org/10.1242/jeb.193.1.1.

Mollo, Ernesto, Angelo Fontana, Vassilios Roussis, Gianluca Polese, Pietro Amodeo, and Michael T. Ghiselin. 2014. "Sensing Marine Biomolecules: Smell, Taste, and the Evolutionary Transition from Aquatic to Terrestrial Life." *Frontiers in Chemistry* 2:92. https://doi.org/10.3389/fchem.2014.00092.

Mollo, Ernesto, M. J. Garson, Gianluca Polese, Pietro Amodeo, and Michael T. Ghiselin. 2017. "Taste and Smell in Aquatic and Terrestrial Environments." *Natural Product Reports* 34 (5): 496–513. https://doi.org/10.1039/C7NP00008A.

Moody, M. F., and J. R. Parriss. 1961. "The Discrimination of Polarized Light by *Octopus*: A Behavioural and Morphological Study." *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 44 (3): 268–291. https://doi.org/10.1007/BF00298356.

Morse, Peter. 2008. "Female Mating Preference Polyandry and Paternity Bias in *Octopus tetricus*." Honours thesis, The University of Western Australia. http://doi.org/10.13140/RG.2.1.4113.6084.

Morse, Peter, and Christine L. Huffard. 2019. "Tactical Tentacles: New Insights on the Processes of Sexual Selection Among the Cephalopoda." *Frontiers in Physiology* 10:1035. https://doi.org/10.3389/fphys.2019.01035.

Morse, Peter, and Christine L. Huffard. 2022. “Chemotactile Social Recognition in the Blue-Ringed Octopus, *Hapalochlaena maculosa*.” *Marine Biology* 169 (8): 99. https://doi.org/10.1007/s00227-022-04087-y.

Morse, Peter, Christine L. Huffard, Mark G. Meekan, Mark I. McCormick, and Kyall R. Zenger. 2018. “Mating Behaviour and Postcopulatory Fertilization Patterns in the Southern Blue-Ringed Octopus, *Hapalochlaena maculosa*.” *Animal Behaviour* 136 (February): 41–51. https://doi.org/10.1016/j.anbehav.2017.12.004.

Morse, Peter, Kyall R. Zenger, Mark I. McCormick, Mark G. Meekan, and Christine L. Huffard. 2017. “Chemical Cues Correlate with Agonistic Behaviour and Female Mate Choice in the Southern Blue-Ringed Octopus, *Hapalochlaena maculosa* (Hoyle, 1883) (Cephalopoda: Octopodidae).” *Journal of Molluscan Studies* 83 (1): 79–87. https://doi.org/10.1093/mollus/eyw045.

Packard, A. 1972. “Cephalopods and Fish: The Limits of Convergence.” *Biological Reviews* 47 (2): 241–307. https://doi.org/10.1111/j.1469-185X.1972.tb00975.x.

Packard, A., Hans Erik Karlsen, and O. Sand. 1990. “Low Frequency Hearing in Cephalopods.” *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*. 166 (4): 501–505. https://doi.org/10.1007/BF00192020.

Polese, Gianluca, Carla Bertapelle, and Anna Di Cosmo. 2015. “Role of Olfaction in *Octopus vulgaris* Reproduction.” *General and Comparative Endocrinology*. 210:55–62. https://doi.org/10.1016/j.ygcen.2014.10.006.

Preuss, T., and Bernd U. Budelmann. 1995. “Proprioceptive Hair Cells on the Neck of the Squid *Lolliguncula brevis*: A Sense Organ in Cephalopods for the Control of Head-to-Body Position.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 349 (1328): 153–178. https://doi.org/10.1098/rstb.1995.0101.

Putland, Rosalyn L., T. Aran Mooney, and Allen F. Mensinger. 2023. “Vessel Sound Causes Hearing Loss for Hummingbird Bobtail Squid (*Euprymna berryi*).” *Frontiers in Marine Science* 10:1151605. https://doi.org/10.3389/fmars.2023.1151605.

Ramirez, M. Desmond, and Todd H. Oakley. 2015. “Eye-Independent, Light-Activated Chromatophore Expansion (LACE) and Expression of Phototransduction Genes in the Skin of *Octopus bimaculoides*.” *Journal of Experimental Biology* 218 (10): 1513–1520. https://doi.org/10.1242/jeb.110908.

Ruth, Peter, Henrike Schmidtberg, Bettina Westermann, and Rudolf Schipp. 2002. “The Sensory Epithelium of the Tentacles and the Rhinophore of *Nautilus pompilius* L. (Cephalopoda, Nautiloidea).” *Journal of Morphology* 251 (3): 239–255. https://doi.org/10.1002/jmor.1086.

Samson, Julia E., T. Aran Mooney, Sander W. S. Gussekloo, and Roger T. Hanlon. 2016. “A Brief Review of Cephalopod Behavioral Responses to Sound.” In *The Effects of Noise on Aquatic Life II*, edited by Arthur N. Popper and Anthony Hawkins. Advances in Experimental Medicine and Biology 875. Springer.

Schnell, Alexandra K., and Nicola S. Clayton. 2019. “Cephalopod Cognition.” *Current Biology* 29 (15): R726–R732. https://doi.org/10.1016/j.cub.2019.06.049.

Seidou, Masatsugu, Michio Sugahara, Hisatoshi Uchiyama, et al. 1990. “On the Three Visual Pigments in the Retina of the Firefly Squid, *Watasenia scintillans*.” *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 166 (6): 769–773. https://doi.org/10.1007/BF00187321.

Serb, Jeanne M., and Douglas J. Eernisse. 2008. “Charting Evolution’s Trajectory: Using Molluscan Eye Diversity to Understand Parallel and Convergent Evolution.” In “The Evolution of Eyes.” Special issue, *Evolution: Education and Outreach* 1 (4): 439–447. https://doi.org/10.1007/s12052-008-0084-1.

Shashar, Nadav, and Thomas W. Cronin. 1996. “Polarization Contrast Vision in Octopus.” *Journal of Experimental Biology* 199 (4): 999–1004. https://doi.org/10.1242/jeb.199.4.999.

Shashar, Nadav, Phillip S. Rutledge, and Thomas W. Cronin. 1996. “Polarization Vision in Cuttlefish—a Concealed Communication Channel?” *Journal of Experimental Biology* 199 (9): 2077–2084. https://doi.org/10.1242/jeb.199.9.2077.

Stubbs, Alexander L., and Christopher W. Stubbs. 2016. “Spectral Discrimination in Color Blind Animals via Chromatic Aberration and Pupil Shape.” *Proceedings of the National Academy of Sciences* 113 (29): 8206–8211. https://doi.org/10.1073/pnas.1524578113.

Sundermann, Gudrun. 1983. “The Fine Structure of Epidermal Lines on Arms and Head of Postembryonic *Sepia officinalis* and *Loligo vulgaris* (Mollusca, Cephalopoda).” *Cell and Tissue Research* 232 (3): 669–677. https://doi.org/10.1007/BF00216437.

Talbot, Christopher M., and Justin N. Marshall. 2011. “The Retinal Topography of Three Species of Coleoid Cephalopod: Significance for Perception of Polarized Light.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 366 (1565): 724–733. https://doi.org/10.1098/rstb.2010.0254.

Tricarico, Elena, Luciana Borrelli, Francesca Gherardi, and Graziano Fiorito. 2011. “I Know My Neighbour: Individual Recognition in *Octopus vulgaris*.” *PLOS ONE* 6 (4): e18710. https://doi.org/10.1371/journal.pone.0018710.

van Giesen, Lena, Peter B. Kilian, Corey A. H. Allard, and Nicholas W. Bellono. 2020. “Molecular Basis of Chemotactile Sensation in Octopus.” *Cell* 183 (3): 594–604.e14. https://doi.org/10.1016/j.cell.2020.09.008.

Voight, Janet R. 1991. “Ligula Length and Courtship in *Octopus digueti*: A Potential Mechanism of Mate Choice.” *Evolution* 45 (7): 1726–1730. https://doi.org/10.1111/j.1558-5646.1991.tb02680.x.

Walderon, Matthew D., Kevin J. Nolt, Robert E. Haas, et al. 2011. “Distance Chemoreception and the Detection of Conspecifics in *Octopus bimaculoides*.” *Journal of Molluscan Studies* 77 (3): 309–311. https://doi.org/10.1093/mollus/eyr009.

Wells, M. J., and J. Wells. 1972. “Sexual Displays and Mating of *Octopus vulgaris* Cuvier and *O. cyanea* Gray and Attempts to Alter Performance by Manipulating the Glandular Condition of the Animals.” *Animal Behaviour* 20 (2): 293–308. https://doi.org/10.1016/S0003-3472(72)80051-4.

Williamson, R. 1988. “Vibration Sensitivity in the Statocyst of the Northern Octopus, *Eledone cirrosa*.” *Journal of Experimental Biology* 134 (1): 451–454. https://doi.org/10.1242/jeb.134.1.451.

Wilson, Maria, Jens Ådne Rekkedal Haga, and Hans Erik Karlsen. 2018. “Behavioural Responses to Infrasonic Particle Acceleration in Cuttlefish.” *Journal of Experimental Biology* 221 (1): jeb166074. https://doi.org/10.1242/jeb.166074.

York, Carly A. 2022. “Cephalopod Sensory Systems.” In *Encyclopedia of Animal Cognition and Behavior*, edited by Jennifer Vonk and Todd K. Shackelford. Springer.

Young, J. Z. 1960. “The Statocysts of *Octopus vulgaris*.” *Proceedings of the Royal Society of London. Series B, Biological Sciences* 152 (946): 3–29. https://doi.org/10.1098/rspb.1960.0019.

CHAPTER 3

Problem-Solving and Intelligence

Problem-solving includes both “the use of novel means to reach a goal when direct means are unavailable”[1] and “the ability to overcome obstacles and achieve a goal”.[2] It takes many different forms in different animals. It can serve many different purposes too, although many of these purposes have some connection to finding and processing food. Some of the most famous examples involve tool use. Chimpanzees[3] and capuchin monkeys[4] use stones to crack nuts, while New Caledonian crows used hooked sticks to extract insects from crevices.[5] But invertebrates solve problems too: think, for example, of leafcutter ants, which overcome many kinds of physical barriers when transporting leaf fragments back to their nests.[6]

Although problem-solving is often regarded as a hallmark of intelligence, the link is not straightforward. When an animal solves a problem, it will not always be because they have understood its structure and come up with a novel, creative solution. Animals often face similar problems over and over again in their lifetimes, and these problems also recur over generations, allowing both learning and evolution to shape solutions without the animal having to comprehend what is going on.[7],[8] Research in primates and birds has tried to pin down the role of understanding and insight by presenting animals with tasks neither they nor their ancestors will have previously encountered in the wild. These tasks usually require the animals to retrieve a bait that is not directly accessible, because it is either placed at a distance (requiring a tool to reach it) or else hidden inside a puzzle box which must first be opened.[1],[9],[10],[11] Of course, while these exact puzzles would never be encountered in the wild, relevantly similar puzzles might be, leading to frequent debate about whether animals are really coming up with innovative, new solutions or using evolved behavioral strategies.

Do cephalopods have problem-solving abilities? Several lines of evidence indicate that octopuses can solve an impressive range of problems. Octopuses exhibit remarkable skill in feeding on bivalves and other shelled prey. They use their suckered arms to pull open the valves or, alternatively, employ their chitinous beak to drill holes through the shell and inject paralyzing toxins into the prey.[12],[13],[14],[15] Importantly, octopuses appear to select the most effective strategy according to the size and species of the prey, showing cognitive flexibility.[13],[16] When they opt to drill holes, the holes are not just drilled at random spots on the shell. Instead, the location of drilling varies depending on the shape of the shell, often matching the position of the adductor muscles or the heart to optimize the effects of the toxins.[17],[18]

Do octopuses ever use tools to open bivalves? In 1857, a naturalist reported observing common octopuses (*Octopus vulgaris*) placing a pebble in between the two valves of a large clam (*Pinna nobilis*) to prevent the closure of the shell and gain access to the prey.[19] Tantalizingly, this behavior has never been conclusively demonstrated. However, octopuses are known to use tools for defense. They have been documented using stones to barricade the entrance of a shelter[20] and using coconut shells to create a portable den that can be disassembled and assembled as required.[21] Octopuses, squid, and cuttlefish all squirt water jets from their funnel to aid burrowing in the sand or to move away food debris, using these jets of water as a tool.[22]

Octopuses also exhibit problem-solving abilities also when confronted with artificial tasks. As long ago as 1911, it was shown that common octopuses can lift a clear cylinder to retrieve baits placed inside.[23],[24] Follow-up experiments demonstrated that octopuses can remove plugs from jars and use a variety of strategies, including pulling and unscrewing lids, to acquire hidden food rewards.[25],[26],[27],[28] Typically, octopuses solve these puzzles through the concerted action of their arms and suckers, without visual access to the apparatus or the prey when it is being manipulated. This behavior resembles the so-called "speculative pounce" seen in the wild, a foraging strategy whereby the octopus envelops a large rock and blindly explores its crevices, using chemical and tactile information acquired through the suckers to locate prey.[29] Yet octopuses can use vision to guide their puzzle-solving too, where appropriate. With precise, visually-guided movements of a single arm, they are able to reach a goal in a three-choice maze[30] and to ambush shrimps.[31]

What mechanisms are behind these impressive displays of problem solving?. The similarities between the "speculative pounce" and the way octopuses approach problem-solving tasks in the lab suggest that hardwired behavioral adaptations may be part of the story.[32] However, their performance often improves progressively over trials (e.g., they open jars more quickly after repeated encounters), indicating that learning is also involved.[25] In support of this idea, there is evidence that scopolamine (a substance known to affect short-term memory) transiently impairs the ability to open jars in trained octopuses, and does so without affecting their predatory responses.[33]

In addition to learning and instinct, though, there is probably also some role for understanding and insight. A 2016 experiment tested whether common octopuses could retrieve a L-shaped food container placed behind a plastic wall through a small hole. Success required rotating the L-shaped object at just the right moment. The researchers found that the octopuses' not only performed well at the original task, but also adapted very quickly to new variations, such as a change in the orientation of the object. This level of flexibility could not be explained by fixed strategies or by simple learning mechanisms, the researchers argued. It could only be explained by understanding the physical requirements of the task.[34]

Yet more evidence of problem-solving in cephalopods comes from “detour” experiments, which investigate the animals’ ability to overcome physical barriers to reach a goal. For instance, a 2017 study allowed cuttlefish (*Sepia gibba* and *Sepia officinalis*) to learn the position of a shelter within their tank. The researchers then added rock barriers to block the direct path to the shelter. They found that animals could perform both horizontal and vertical detours to reach the goal.[35] Reports from the wild provide further evidence of an ability to plan detours around obstacles. For instance, divers have observed a cuttlefish (*S. officinalis*) swimming vertically over a 3 m wall and moving straight towards a small crevice behind the wall to hide.[36] The direct path taken, plus the apparent lack of any hesitation, suggested the animal was returning to a familiar location via a pre-planned route. Octopuses have been seen performing similar feats.[37],[38] In the lab, octopuses have performed well in detour tasks using food, rather than a shelter, as a goal.[39],[40],[41],[42],[43] For more on the navigation abilities of cephalopods, see “Navigating the Environment.”

In sum, cephalopods can solve various physical problems. The evidence available is largely based on the common octopus and a few other species. In the future, the testing of currently overlooked species, including squids and nautiluses, may allow a richer picture of problem-solving in cephalopods.[44]

References

1 a b Seed and Call 2010

2 Chow et al. 2016

3 Boesch and Boesch 1982

4 Fragaszy et al. 2004

5 Hunt and Gray 2004

6 Dussutour et al. 2009

7 Amodio et al. 2018

8 Shettleworth 2010

9 Mulcahy and Call 2006

10 Jacobs and Osvath 2015

11 Jelbert et al. 2015

12 Nixon and Maconnachie 1988

13 a b McQuaid 1994

14 Fiorito and Gherardi 1999

15 Hanlon and Messenger 2018

16 Wodinsky 1969

17 Steer and Semmens 2003

18 Anderson and Mather 2007

19 Power 1857

20 Mather 1994

21 Finn et al. 2009

22 Mather 2021

23 Piéron 1911

24 Boycott 1954

25 a b Fiorito et al. 1990

26 Anderson and Mather 2010

27 Borrelli et al. 2020

28 Maselli et al. 2020

29 Yarnall 1969

30 Gutnick et al. 2011

31 Caldwell et al. 2015

32 Fiorito, Biederman, et al. 1998

33 Fiorito, Agnisola, et al. 1998

34 Richter et al. 2016

35 Scatà et al. 2017

36 Jozet-Alves et al. 2014

37 Mather 1991

38 Forsythe and Hanlon 1997

39 Schiller 1949

40 Wells 1964

41 Wells 1967

42 Wells 1970

43 Moriyama and Gunji 1997

44 Amodio et al. 2019

Key Texts

Amodio, Piero, Markus Boeckle, Alexandra K. Schnell, Ljerka Ostojíc, Graziano Fiorito, and Nicola S. Clayton. 2019. "Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence?" *Trends in Ecology and Evolution* 34 (1): 45–56. https://doi.org/10.1016/j.tree.2018.10.010.

A theoretical paper providing testable predictions about the factors that may have shaped the evolution of complex cognition in cephalopods.

Finn, Julian K., Tom Tregenza, and Mark D. Norman. 2009. "Defensive Tool Use in a Coconut-Carrying Octopus." *Current Biology* 19 (23): R1069–R1070. https://doi.org/10.1016/j.cub.2009.10.052.

This study reveals that veined octopuses assemble composite tools for defense and even carry these objects for future usage.

Fiorito, Graziano, Christoph von Planta, and Pietro Scotto. 1990. "Problem Solving Ability of *Octopus vulgaris* Lamarck (Mollusca, Cephalopoda)." *Behavioral and Neural Biology* 53 (2): 217–230. https://doi.org/10.1016/0163-1047(90)90441-8.

This study showed that octopuses can remove plugs from jars to acquire a hidden prey, thereby also providing a flexible paradigm to investigate problem solving in the octopus.

Gutnick, Tamar, Ruth A. Byrne, Binyamin Hochner, and Michael J. Kuba. 2011. "*Octopus vulgaris* Uses Visual Information to Determine the Location of Its Arm." *Current Biology* 21 (6): 460–462. https://doi.org/10.1016/j.cub.2011.01.052.

This study demonstrates that octopuses can perform precise and goal-directed movements of a single arm by integrating visual cues and peripheral arm location information.

Richter, Jonas N., Binyamin Hochner, and Michael J. Kuba. 2016. "Pull or Push? Octopuses Solve a Puzzle Problem." *PLOS ONE* 11 (3): e0152048. https://doi.org/10.1371/journal.pone.0152048.

This study indicates that octopus' problem-solving abilities involve impressive levels of behavioral flexibility, suggesting they are able to understand aspects of the problem and generalize these to new situations.

Bibliography

Alves, Christelle, Jean Geary Boal, and Ludovic Dickel. 2008. “Short-Distance Navigation in Cephalopods: A Review and Synthesis.” In “Spatial Navigation,” edited by Demis Basso. Special issue, *Cognitive Processing* 9 (4): 239–247. https://doi.org/10.1007/s10339-007-0192-9.

Amodio, Piero, Markus Boeckle, Alexandra K. Schnell, Ljerka Ostojíc, Graziano Fiorito, and Nicola S. Clayton. 2019. “Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence?” *Trends in Ecology and Evolution* 34 (1): 45–56. https://doi.org/10.1016/j.tree.2018.10.010.

Amodio, Piero, Sarah A. Jelbert, and Nicola S. Clayton. 2018. “The Interplay Between Psychological Predispositions and Skill Learning in the Evolution of Tool Use.” In “Habits and Skills,” edited by Joern Diedrichsen and Barbara Knowlton. Special Issue, *Current Opinion in Behavioral Sciences* 20 (April): 130–137. https://doi.org/10.1016/j.cobeha.2018.01.002.

Anderson, Roland C., and Jennifer A. Mather. 2007. “The Packaging Problem: Bivalve Prey Selection and Prey Entry Techniques of the Octopus *Enteroctopus dofleini*.” *Journal of Comparative Psychology* 121 (3): 300–305. https://doi.org/10.1037/0735-7036.121.3.300.

Anderson, Roland C., and Jennifer A. Mather. 2010. “It’s All in the Cues: Octopuses (*Enteroctopus dofleini*) Learn to Open Jars.” In *Proceedings of the 3rd International Symposium Coleoid Cephalopods Through Time*, edited by Dirk Fuchs. Ferrantia 59. Musée National d’Histoire Naturelle Luxembourg. https://ps.mnhn.lu/ferrantia/publications/Ferrantia59.pdf.

Benson-Amram, Sarah, and Kay E. Holekamp. 2012. “Innovative Problem Solving by Wild spotted Hyenas.” *Proceedings of the Royal Society B: Biological Sciences* 279 (1744): 4087–4095. https://doi.org/10.1098/rspb.2012.1450.

Boesch, Christophe, and Hedwige Boesch. 1982. “Optimisation of Nut-Cracking with Natural Hammers by Wild Chimpanzees.” *Behaviour* 83 (3–4): 265–286. https://doi.org/10.1163/156853983X00192.

Borrelli, Luciana, Cinzia Chiandetti, and Graziano Fiorito. 2020. “A Standardized Battery of Tests to Measure *Octopus vulgaris*’ Behavioural Performance.” *Invertebrate Neuroscience* 20 (1): 4. https://doi.org/10.1007/s10158-020-0237-7.

Boycott, B. B. 1954. “Learning in *Octopus vulgaris* and Other Cephalopods.” *Pubblicazioni Stazione Zoologica di Napoli* 25:67–93.

Caldwell, Roy L., Richard Ross, Arcadio Rodaniche, and Christine L. Huffard. 2015. “Behavior and Body Patterns of the Larger Pacific Striped Octopus.” *PLOS ONE* 10 (8): e0134152. https://doi.org/10.1371/journal.pone.0134152.

Chow, Pizza Ka Yee, Stephen E. G. Lea, Natalie Hempel de Ibarra, and Théo Robert. 2017. “How to Stay Perfect: The Role of Memory and Behavioural Traits in an Experienced Problem and a Similar Problem.” *Animal Cognition* 20 (5): 941–952. https://doi.org/10.1007/s10071-017-1113-7.

Chow, Pizza Ka Yee, Stephen E. G. Lea, and Lisa A. Leaver. 2016. “How Practice Makes Perfect: The Role of Persistence, Flexibility and Learning in Problem-Solving Efficiency.” *Animal Behaviour* 112 (February): 273–283. https://doi.org/10.1016/j.anbehav.2015.11.014.

Damerius, Laura A., Sereina M. Graber, Erik P. Willems, and Carel P. van Schaik. 2017. “Curiosity Boosts Orang-Utan Problem-Solving Ability.” *Animal Behaviour* 134 (December): 57–70. https://doi.org/10.1016/j.anbehav.2017.10.005.

DeCasien, Alex R., Scott A. Williams, and James P. Higham. 2017. “Primate Brain Size Is Predicted by Diet but Not Sociality.” *Nature Ecology & Evolution* 1 (5): 112. https://doi.org/10.1038/s41559-017-0112.

Dunbar, R. I. M., and Susanne Shultz. 2017. “Why Are There So Many Explanations for Primate Brain Evolution?” *Philosophical Transactions of the Royal Society B: Biological Sciences* 372 (1727): 20160244. https://doi.org/10.1098/rstb.2016.0244.

Dussutour, Audrey, Jean-Louis Deneubourg, Samuel Beshers, and Vincent Fourcassié. 2009. “Individual and Collective Problem-Solving in a Foraging Context in the Leaf-Cutting Ant *Atta colombica*.” *Animal Cognition* 12 (1): 21–30. https://doi.org/10.1007/s10071-008-0165-0.

Finn, Julian K., Tom Tregenza, and Mark D. Norman. 2009. “Defensive Tool Use in a Coconut-Carrying Octopus.” *Current Biology* 19 (23): R1069–R1070. https://doi.org/10.1016/j.cub.2009.10.052.

Fiorito, Graziano, Claudio Agnisola, M. d’Addio, A. Valanzano, and G. Calamandrei. 1998. “Scopolamine Impairs Memory Recall in *Octopus vulgaris*.”*Neuroscience Letters* 253 (2): 87–90. https://doi.org/10.1016/S0304-3940(98)00611-9.

Fiorito, Graziano, G. B. Biederman, Valerie A. Davey, and Francesca Gherardi. 1998. “The Role of Stimulus Preexposure in Problem Solving by *Octopus vulgaris*.” *Animal Cognition* 1 (2): 107–112. https://doi.org/10.1007/s100710050015.

Fiorito, Graziano, and Francesca Gherardi. 1999. “Prey-Handling Behaviour of *Octopus vulgaris* (Mollusca, Cephalopoda) on Bivalve Preys.” *Behavioural Processes* 46 (1): 75–88. https://doi.org/10.1016/S0376-6357(99)00020-0.

Fiorito, Graziano, Christoph von Planta, and Pietro Scotto. 1990. “Problem Solving Ability of *Octopus vulgaris* Lamarck (Mollusca, Cephalopoda).” *Behavioral and Neural Biology* 53 (2): 217–230. https://doi.org/10.1016/0163-1047(90)90441-8.

Forsythe, John W., and Roger T. Hanlon. 1997. “Foraging and Associated Behavior by *Octopus cyanea* Gray, 1849 on a Coral Atoll, French Polynesia.” *Journal of Experimental Marine Biology and Ecology* 209 (1–2): 15–31. https://doi.org/10.1016/S0022-0981(96)00057-3.

Fragaszy, Dorothy, Patrícia Izar, Elisabetta Visalberghi, Eduardo B. Ottoni, and Marino Gomes de Oliveira. 2004. “Wild Capuchin Monkeys (*Cebus libidinosus*) Use Anvils and Stone Pounding Tools.” *American Journal of Primatology* 64 (4): 359–366. https://doi.org/10.1002/ajp.20085.

Gutnick, Tamar, Ruth A. Byrne, Binyamin Hochner, and Michael J. Kuba. 2011. “*Octopus vulgaris* Uses Visual Information to Determine the Location of Its Arm.” *Current Biology* 21 (6): 460–462. https://doi.org/10.1016/j.cub.2011.01.052.

Hanlon, Roger T., and John B. Messenger. 2018. *Cephalopod Behaviour*. 2nd ed. Cambridge University Press.

Hunt, Gavin R., and Russell D. Gray. 2004. “The Crafting of Hook Tools by Wild New Caledonian Crows.” Supplement, *Proceedings of the Royal Society B: Biological Sciences* 271 (S3): S88–S90. https://doi.org/10.1098/rsbl.2003.0085.

Isler, Karin, and Carel P. van Schaik. 2006. “Metabolic Costs of Brain Size Evolution.” *Biology Letters* 2 (4): 557–560. https://doi.org/10.1098/rsbl.2006.0538.

Jacobs, Ivo F., and Mathias Osvath. 2015. “The String-Pulling Paradigm in Comparative Psychology.” *Journal of Comparative Psychology* 129 (2): 89–120. https://doi.org/10.1037/a0038746.

Jelbert, Sarah A., Alex H. Taylor, and Russell D. Gray. 2015. “Investigating Animal Cognition with the Aesop’s Fable Paradigm: Current Understanding and Future Directions.” *Communicative & Integrative Biology* 8 (4): 1035846. https://doi.org/10.1080/19420889.2015.1035846.

Jozet-Alves, Christelle, Anne-Sophie Darmaillacq, and Jean Geary Boal. 2014. “Navigation in Cephalopods.” In *Cephalopod Cognition*, edited by Anne-Sophie Darmaillacq, Ludovic Dickel, and Jennifer A. Mather. Cambridge University Press.

Maselli, Valeria, Al-Sayed Al-Soudy, Maria Buglione, Massimo Aria, Gianluca Polese, and Anna Di Cosmo. 2020. “Sensorial Hierarchy in *Octopus vulgaris*’s Food Choice: Chemical vs. Visual.” *Animals* 10 (3): 457. https://doi.org/10.3390/ani10030457.

Mather, Jennifer A. 1991. "Navigation by Spatial Memory and Use of Visual Landmarks in Octopuses." *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 168 (4): 491–497. https://doi.org/10.1007/BF00199609.

Mather, Jennifer A. 1994. "'Home' Choice and Modification by Juvenile *Octopus vulgaris* (Mollusca: Cephalopoda): Specialized Intelligence and Tool Use?" *Journal of Zoology* 233 (3): 359–368. https://doi.org/10.1111/j.1469-7998.1994.tb05270.x.

Mather, Jennifer A. 2021. "Cephalopod Tool Use." In *Encyclopedia of Evolutionary Psychological Science*, edited by Todd K. Shackelford and Viviana A Weekes-Shackelford. Springer.

McQuaid, C. D. 1994. "Feeding Behaviour and Selection of Bivalve Prey by *Octopus vulgaris* Cuvier". *Journal of Experimental Marine Biology and Ecology* 177 (2) 187–202. https://doi.org/10.1016/0022-0981(94)90236-4.

Miller, Rachael, Sarah A. Jelbert, Alex H. Taylor, et al. 2016. "Performance in Object-Choice Aesop's Fable Tasks Are Influenced by Object Biases in New Caledonian Crows but Not in Human Children." *PLOS ONE* 11 (12): e0168056. https://doi.org/10.1371/journal.pone.0168056.

Moriyama, Tohru, and Yukio-Pegio Gunji. 1997. "Autonomous Learning in Maze Solution by *Octopus*." *Ethology* 103 (6): 499–513. https://doi.org/10.1111/j.1439-0310.1997.tb00163.x.

Mulcahy, Nicholas J., and Josep Call. 2006. "How Great Apes Perform on a Modified Trap-Tube Task." *Animal Cognition* 9 (3): 193–199. https://doi.org/10.1007/s10071-006-0019-6.

Nixon, Marion, and Elaine Maconnachie. 1988. "Drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Mediterranean." *Journal of Zoology* 216 (4): 687–716. https://doi.org/10.1111/j.1469-7998.1988.tb02466.x.

Piéron, Henri. 1911. "Contribution à la psychologie du poulpe." *Bulletins de l'Institut Général Psychologique* 11 (2): 111–119.

Power, Jeannette. 1857. "Observations on the Habits of Various Marine Animals." *Annals and Magazine of Natural History,* 2nd ser., 20 (119): 334–336. https://www.biodiversitylibrary.org/item/61789.

Richter, Jonas N., Binyamin Hochner, and Michael J. Kuba. 2016. "Pull or Push? Octopuses Solve a Puzzle Problem." *PLOS ONE* 11 (3): e0152048. https://doi.org/10.1371/journal.pone.0152048.

Rosati, Alexandra G. 2017. "Foraging Cognition: Reviving the Ecological Intelligence Hypothesis." *Trends in Cognitive Sciences* 21 (9): 691–702. https://doi.org/10.1016/j.tics.2017.05.011.

Rowell, Misha K., Neville Pillay, and Tasmin L. Rymer. 2021. "Problem Solving in Animals: Proposal for an Ontogenetic Perspective." *Animals* 11 (3): 866. https://doi.org/10.3390/ani11030866.

Scatà, Gabriella, Anne-Sophie Darmaillacq, Ludovic Dickel, Steve McCusker, and Nadav Shashar. 2017. “Going Up or Sideways? Perception of Space and Obstacles Negotiating by Cuttlefish.” *Frontiers in Physiology* 8:173. https://doi.org/10.3389/fphys.2017.00173.

Schiller, Paul H. 1949. “Delayed Detour Response in the Octopus.” *Journal of Comparative and Physiological Psychology* 42 (3): 220–225. https://doi.org/10.1037/h0056879.

Seed, Amanda M., and Josep Call. 2010. “Problem-Solving in Tool-Using and Non-Tool-Using Animals” In *Encyclopedia of Animal Behavior*, edited by Michael D. Breed and Janice Moore. Elsevier.

Shettleworth, Sara J. 2010. “Clever Animals and Killjoy Explanations in Comparative Psychology.” *Trends in Cognitive Sciences* 14 (11): 477–481. https://doi.org/10.1016/j.tics.2010.07.002.

Steer, Mike A., and Jayson M. Semmens. 2003. “Pulling or Drilling, Does Size or Species Matter? An Experimental Study of Prey Handling in *Octopus dierythraeus* (Norman, 1992).” *Journal of Experimental Marine Biology and Ecology* 290 (2): 165–178. https://doi.org/10.1016/S0022-0981(03)00076-5.

van Woerden, Anneke T., Erik P. Willems, Carel P. van Schaik, and Karin Isler. 2012. “Large Brains Buffer Energetic Effects of Seasonal Habitats in Catarrhine Primates.” *Evolution* 66 (1): 191–199. https://doi.org/10.1111/j.1558-5646.2011.01434.x.

Visalberghi, Elisabetta, and M. Tomasello. 1998. “Primate Causal Understanding in the Physical and Psychological Domains.” *Behavioural Processes* 42 (2–3): 189–203. https://doi.org/10.1016/S0376-6357(97)00076-4.

Wells, M. J. 1964. “Detour Experiments with Octopuses.” *Journal of Experimental Biology* 41 (3): 621–642. https://doi.org/10.1242/jeb.41.3.621.

Wells, M. J. 1967. “Short-Term Learning and Interocular Transfer in Detour Experiments with Octopuses.” *Journal of Experimental Biology* 47 (3): 393–408. https://doi.org/10.1242/jeb.47.3.393.

Wells, M. J. 1970. “Detour Experiments with Split-Brain Octopuses.” *Journal of Experimental Biology* 53 (2): 375–389. https://doi.org/10.1242/jeb.53.2.375.

Wodinsky, Jerome. 1969. “Penetration of the Shell and Feeding on Gastropods by *Octopus*.” *American Zoologist* 9 (3): 997–1010. https://doi.org/10.1093/icb/9.3.997.

Yarnall, John L. 1969. “Aspects of the Behaviour of *Octopus cyanea gray*.” *Animal Behaviour* 17 (4): 747–754. https://doi.org/10.1016/S0003-3472(69)80022-9.

CHAPTER 4

Learning and Memory

Octopuses, cuttlefish, and squid (known collectively as the soft-bodied cephalopods or coleoid cephalopods) have areas of their brain dedicated to learning and memory.[1] Their brains are organized profoundly differently from those of vertebrates—they are donut-shaped, forming a ring around the esophagus. They show us that many of the learning and memory abilities found in mammals can also be achieved by a very different brain. By contrast, the nautiloids (which have shells, and so look quite different from soft-bodied cephalopods) possess relatively simple brains, traditionally thought to lack any obvious regions dedicated to learning and memory.[2] Yet they too are still able to succeed in some learning and memory tasks. The learning and memory abilities of cephalopods can broadly be sorted into three categories: “non-associative” (relatively simple), “associative” (associating some things with others), and “temporal” (related to time).

Simple Non-Associative Learning

Two of the simplest kinds of learning are sensitization and habituation. They are called “non-associative” because they do not involve associating one sensory stimulus with another or with an outcome. Sensitization occurs when repeated exposure to the same stimulus results in the animal becoming *more sensitive* to that stimulus, as shown by progressively amplified responses. Habituation, by contrast, occurs when repeated exposure to a stimulus results in the animal becoming *less sensitive* to that stimulus, as shown by a progressively depressed response. Cephalopods display both sensitization and habituation in different contexts.

Squid display what is known as nociceptive sensitization: after a minor injury, squid become much more sensitive to touch.[3] The entire body appears sensitized, with the effect lasting at least 24 hours. This is a sign that they might feel something akin to pain, a possibility discussed in much greater detail in the entry on Pain. Meanwhile, after repeated exposure, octopuses habituate to visual stimuli,[4],[5],[6] cuttlefish habituate to sounds,[7] squid habituate to the presence of a false predator,[8] and nautiloids habituate to unfamiliar environments.[9]

Associative Learning

Octopuses, squid, and cuttlefish can rapidly learn to associate a stimulus with a positive or negative outcome.[10],[11],[12],[13],[14] When learning about visual stimuli, they can make fine discriminations between visual features, taking account of shape, size, brightness, and orientation (Figure 14).[15],[16],[17],[18],[19],[20] Octopuses can even learn to distinguish between objects differing in their texture-taste combination (an ability known as "chemotactile" discrimination).[21],[22],[23] Octopuses and cuttlefish can also reverse a previously learned association: they can learn that a stimulus that used to predict a reward now predicts punishment, and vice versa.[24],[25],[26],[27],[28] One particular experimental design, the "prawn-in-the-tube" test, has revealed intricate details about how associations are made during associative learning tasks.[14],[29],[30] In this experimental set-up, cuttlefish are presented with a prawn in a glass tube. Through a blend of tactile and visual sensory cues, they learn that the prey is inaccessible due to the glass barrier (Figure 15).

Cephalopods are also capable of learning about spatial features of their environment, such as the locations of dens and other important objects. For example, cuttlefish can locate shelter within a maze.[31] To find their way around, they sometimes use the orientation of polarized light and sometimes use information about landmarks.[30] When one source of information becomes unavailable, they can switch to using the other. Meanwhile, octopuses can return directly to their den after a meandering foraging trip.[32],[33],[34]

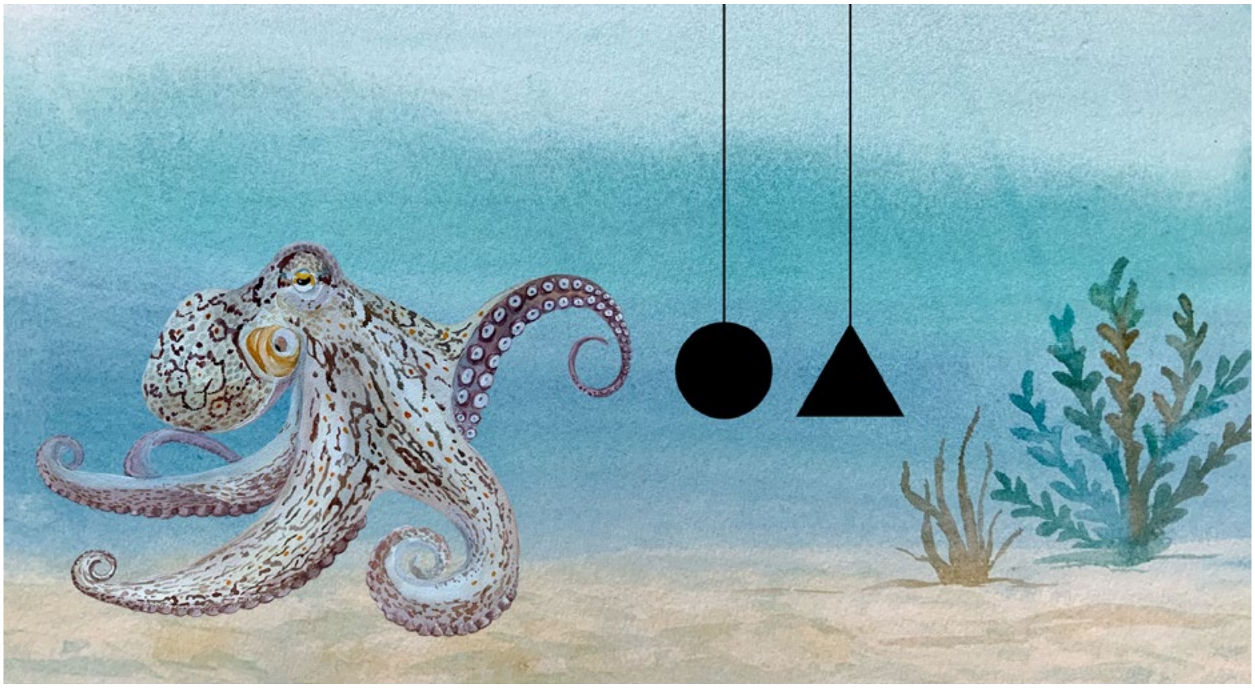

FIGURE 14. Illustration of a discrimination task in which an octopus needs to learn to distinguish between two different shapes, a circle and a triangle.

Like us, cephalopods possess both short- and long-term memory. The nature of these memory abilities varies between cephalopod species. Octopuses and cuttlefish can remember learned information for weeks[33] and bobtail squids have stable long-term memory that lasts at least 12 days,[13] whereas nautiluses do not appear to retain information beyond 24 hours.[35]

Learning about Time

In temporal forms of learning and memory, an animal must keep track of time and update their decision-making with new information about what happened, where, and when.[36] Keeping track of time is vital for some cognitively advanced animals to flexibly adjust their foraging behavior, especially when storing food that can decay or hunting prey that becomes available at different rates.[37] The distinction between associative and temporal learning is not a sharp one, since the latter will usually involve an element of the former. However, animals go significantly

FIGURE 15. Illustration of the prawn-in-the-tube test in which a cuttlefish is presented with live shrimp inside a glass tube and must learn to inhibit predatory behavior.

beyond associative learning when they are able to recall the detail of a specific, one-off event in their past (such as a specific encounter with a predator, prey animal, or family member) and flexibly make use of that detail to decide what to do in a relevantly similar situation.

For most humans, the ability to remember the fine detail of specific past events (often known as *episodic memory*) involves conscious experience: we re-experience the sights and sounds of past moments in a sort of "mind's eye," where we can recall how things seemed from our point of view at the time in question. In the literature on human psychology, this is sometimes called "autonoetic awareness." Part of the experience is that the event feels like it happened in our past, an elusive feeling called "chronesthesia."[38]

Cuttlefish have been shown to recollect information about the "what, where, and when" of personally experienced events.[39] When looking for prey, they can alter their search strategies depending on *what* they had previously eaten, *where* their previous meal had been sourced, and *when* they last ate (i.e., how much time has passed since their previous meal). In non-human animals, this is often termed “episodic-like memory” because the evidence does not conclusively establish that the kinds of conscious experience involved in human episodic memory are present. We don’t know whether cuttlefish have autonoetic awareness or feel a sense of chronesthesia.

Cuttlefish are also able to retrieve information about the sensory *source* of an episodic-like memory—a capacity referred to as *source memory*. For instance, they make different choices depending on whether they have *seen* or *smelled* the prey item.[40],[41] Unlike in humans and other mammals, the cuttlefish equivalent of episodic memory does not deteriorate with age (though their lifespans are much shorter than ours, usually 1–2 years). Elderly cuttlefish are still able to recall spatial and temporal information to guide their foraging behavior, and this continues until the final weeks of their lives.[42]

Cuttlefish have demonstrated some capacity to *plan for the future*. They can use predictions about the future availability of their preferred prey (i.e., shrimp) to guide their foraging behavior.[40] They reduce their consumption of crabs, their less preferred prey, during the day when they predict shrimp will be available at night.

They can also *delay gratification*, something even humans often find very difficult. When deciding whether a preferred prey item is worth waiting for, cuttlefish will take account of the expected length of the wait (Figure 16).[43] Some animals were able to wait up to 130 seconds, refraining from taking from an immediate but less desirable prey item right in front of them. These wait times are comparable to those observed in apes,[44] parrots,[45] and corvids.[46] Furthermore, cuttlefish can flexibly adjust their self-control behavior in response to changing conditions. When the preferred prey is visible but never obtainable, cuttlefish give up waiting and consume the less preferred prey item almost immediately.[43] For more detail, see “Self-Regulation and Self-Awareness.”

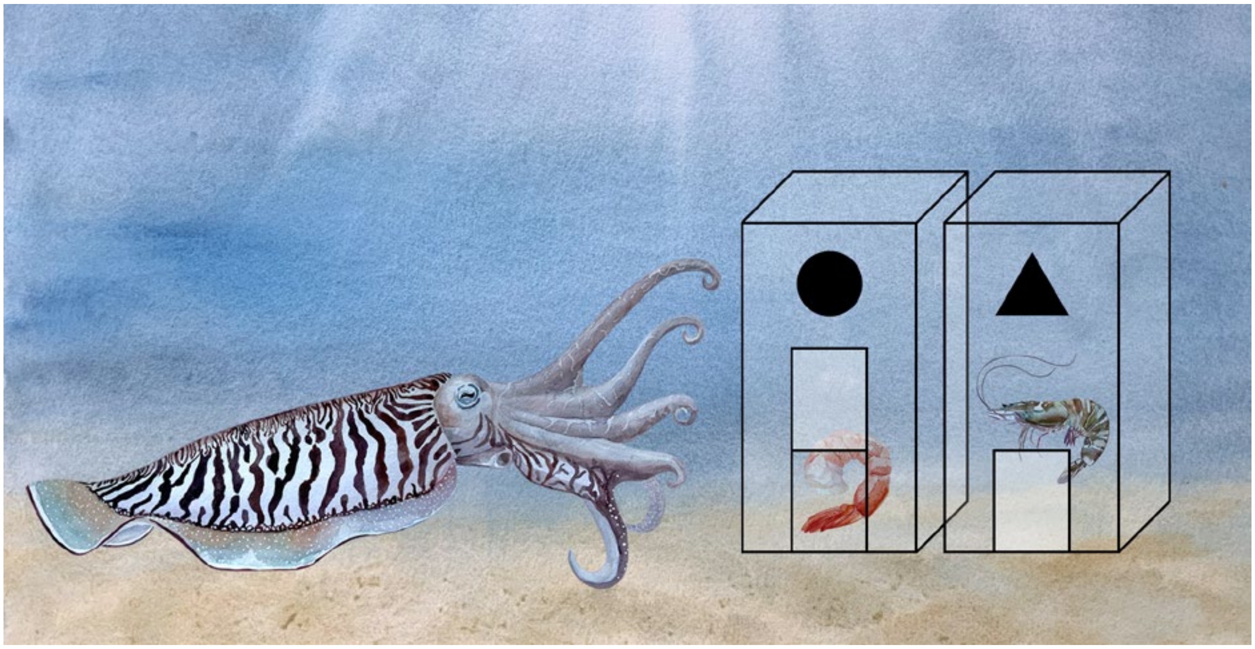

FIGURE 16. Illustration of a delayed gratification task in which a cuttlefish must choose between a less preferred reward—a cooked prawn—available immediately (circle chamber), or wait for a more preferred reward—a live shrimp—available after a time delay (triangle chamber).

There is some evidence that octopuses in the wild remember where they have recently been, and make use of that information. They avoid visiting areas where they recently foraged, presumably having memorized where and when they previously foraged to avoid areas depleted of food.[31],[34] Yet, when presented with an episodic-like memory task, octopuses behave differently from cuttlefish, approaching the task in a different way. They appear to link learned information to the *order* in which different events occurred, attaching more significance to the order of events than to elapsed time intervals.[47]

In short, cephalopods can learn through non-associative, associative, and temporal avenues and possess both short- and long-term memory. Cuttlefish have advanced types of learning and memory once thought to be unique to large-brained vertebrates, and not yet demonstrated in any other invertebrate: episodic-like memory, source memory,[41] and advanced delayed gratification.

References

1 Nixon and Young 2003

2 Young 1965

3 Crook et al. 2013

4 Kuba et al. 2005

5 Kuba et al. 2006

6 Kuba et al. 2007

7 Samson et al. 2014

8 Long et al. 1989

9 Crook et al. 2009

10 Boycott and Young 1950

11 Wells and Young 1968

12 Messenger 1973b

13 a b Zepeda et al. 2017

14 a b Agin et al. 2006

15 Sutherland 1957b

16 Sutherland 1957a

17 Sutherland 1960

18 Sutherland 1963

19 Sutherland et al. 1963

20 Allen et al. 1985

21 Wells 1963

22 Wells 1964b

23 Wells et al. 1965

24 Mackintosh 1962

25 Mackintosh and Mackintosh 1963

26 Mackintosh and Mackintosh 1964

27 Bublitz et al. 2017

28 Bublitz et al. 2021

29 Purdy et al. 2006

30 a b Cartron et al. 2012

31 a b Mather 1991

32 Alves et al. 2007

33 a b Boal et al. 2000

34 a b Forsythe and Hanlon 1997

35 Crook and Basil 2008

36 Clayton and Dickinson 1998

37 Schnell and Clayton 2022

38 Tulving 2005

39 Jozet-Alves et al. 2013

40 a b Billard, Schnell, et al. 2020

41 a b Billard, Clayton, et al. 2020

42 Schnell, Clayton, et al. 2021

43 a b Schnell, Boeckle, et al. 2021

44 Rosati et al. 2007

45 Auersperg et al. 2013

46 Hillemann et al. 2014

47 Poncet et al. 2022

Key Texts

Billard, Pauline, Nicola S. Clayton, and Christelle Jozet-Alves. 2020. "Cuttlefish Retrieve Whether They Smelt or Saw a Previously Encountered Item." *Scientific Reports* 10:5413. https://doi.org/10.1038/s41598-020-62335-x.

This study demonstrates important details about specific features of episodic memories. Results reveal that cuttlefish were able to adjust their foraging behavior by retrieving perceptual features that were tied to the source of a previous foraging event (i.e., whether they had seen the prey item or smelled it).

Cartron, Lelia, Anne-Sophie Darmaillacq, and Ludovic Dickel. 2013. "The Prawn-in-the-Tube procedure: What Do Cuttlefish Learn and Memorize?" *Behavioural Brain Research*, 240 (1): 29–32. https://doi.org/10.1016/j.bbr.2012.11.010.

This study demonstrates key details about how cuttlefish make associations during associative learning tasks.

Crook, Robyn J., Roger T. Hanlon, and Jennifer A. Basil. 2009. "Memory of Visual and Topographical Features Suggests Spatial Learning in Nautilus (*Nautilus pompilius* L.)." *Journal of Comparative Psychology* 123 (3): 264–274. https://doi.org/10.1037/a0015921.

This study indicates that nautiluses navigate using both nearby and distant spatial cues in 2D and 3D spaces. These findings are noteworthy because their performance in these tasks aligns with shell-less cephalopods (octopus, cuttlefish, squid), despite the nautilus having simpler neuroanatomy in comparison.

Jozet-Alves, Christelle, Marion Bertin, and Nicola S. Clayton. 2013. "Evidence of Episodic-Like Memory in Cuttlefish." *Current Biology* 23 (23): R1033–R1035. https://doi.org/10.1016/j.cub.2013.10.021.

This is the first study to demonstrate this type of "personally experienced" memory in any invertebrate animal.

Poncet, Lisa, Coraline Desnous, Cécile Bellanger, and Christelle Jozet-Alves. 2022. "Unruly Octopuses Are the Rule: *Octopus vulgaris* Use Multiple and Individually Variable Strategies in an Episodic-Memory Task." *Journal of Experimental Biology* 225 (19): jeb244234. https://doi.org/10.1242/jeb.244234.

This study emphasizes distinctions in recollection-type memory between octopuses and cuttlefish. Notably, the results suggest that octopuses may employ diverse and flexible strategies when tackling memory tasks rather than applying a fixed solution.

Schnell, Alexandra K., Markus Boeckle, Micaela Rivera, Nicola S. Clayton, and Roger T. Hanlon. 2021. "Cuttlefish Exert Self-Control in a Delay of Gratification Task." *Proceedings of the Royal Society B: Biological Sciences* 288 (1946): 20203161. https://doi.org/10.1098/rspb.2020.3161.

This groundbreaking study demonstrates temporal delayed gratification in an invertebrate, with waiting times comparable to those observed in certain apes and corvids. Furthermore, it established the initial connection between self-control and intelligence beyond the primate lineage.

Schnell, Alexandra K., Nicola S. Clayton, Roger T. Hanlon, and Christelle Jozet-Alves. 2021. “Episodic-Like Memory Is Preserved with Age in Cuttlefish.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1957): 20211052. https://doi.org/10.1098/rspb.2021.1052.

This study reveals further details about episodic-like memory in cuttlefish. Specifically, this type of memory does not appear to deteriorate with age—a contrast to the age-related deterioration observed in humans and other mammals.

Zepeda, Emily A., Robert J. Veline, and Robyn J. Crook. 2017. “Rapid Associative Learning and Stable Long-Term Memory in the Squid *Euprymna scolopes*.” *Biological Bulletin* 232 (3): 212–218. https://doi.org/10.1086/693461.

This study reveals that bobtail squid, less explored compared to octopus and cuttlefish, also exhibit rapid associative learning and retain long-term memory for at least 12 days.

Bibliography

Agin, Véronique, Raymond Chichery, Ludovic Dickel, and Marie-Paule Chichery. 2006. "The Prawn-in-the-Tube Procedure in Cuttlefish: Habituation or Passive Avoidance Learning?" *Learning and Memory* 13 (1): 97–101. https://doi.org/10.1101/lm.90106.

Agin, Véronique, Raymond Chichery, Eric Maubert, and Marie-Paule Chichery. 2003. "Time-Dependent Effects of Cycloheximide on Long-Term Memory in Cuttlefish." *Pharmacology Biochemistry and Behavior* 75 (1): 141–146. https://doi.org/10.1016/S0091-3057(03)00041-8.

Agin, Véronique, Ludovic Dickel, Raymond Chichery, and Marie-Paule Chichery. 1998. "Evidence for a Specific Short-Term Memory in Cuttlefish, *Sepia*." *Behavioural Processes* 43 (3): 329–334. https://doi.org/10.1016/S0376-6357(98)00019-9.

Allen, Anne, Jon Michels, and J. Z. Young. 1985. "Memory and Visual Discrimination by Squids." *Marine Behaviour and Physiology* 11 (4): 271–282. https://doi.org/10.1080/10236248509387052.

Alves, Christelle, Raymond Chichery, Jean Geary Boal, and Ludovic Dickel. 2007. "Orientation in the Cuttlefish *Sepia officinalis*: Response Versus Place Learning." *Animal Cognition* 10 (1): 29–36. https://doi.org/10.1007/s10071-006-0027-6.

Auersperg, A. M. I., I. B. Laumer, and Thomas Bugnyar. 2013. "Goffin Cockatoos Wait for Qualitative and Quantitative Gain but Prefer 'Better' to 'More.'" *Biology Letters* 9 (3): 20121092. https://doi.org/10.1098/rsbl.2012.1092.

Basil, Jennifer A., Gregory J. Barord, Robyn J. Crook, et al. 2012. "A Synthetic Approach to the Study of Learning and Memory in Chambered *Nautilus* L. (Cephalopoda: Nautiloidea)." In "Behaviour in Cephalopods: Underlying Mechanisms and Methodological Approaches," edited by Michael J. Kuba, Tamar Gutnick, and Sigurd von Boletzky. Special issue, *Vie et Milieu / Life and Environment* 61 (4): 231–242.

Basil, Jennifer A., and Robyn J. Crook. 2021. "Learning and Memory in the Living Fossil, Chambered Nautilus." In *Physiology of Molluscs: A Collection of Selected Reviews*, vol. 2, edited by Saber Saleuddin and Spencer Mukai. Apple Academic Press.

Beran, Michael J. 2002. "Maintenance of Self-Imposed Delay of Gratification by Four Chimpanzees (*Pan troglodytes*) and an Organutan (*Pongo pygmaeus*)." *Journal of General Psychology* 129 (1): 49–66. https://doi.org/10.1080/00221300209602032.

Billard, Pauline, Nicola S. Clayton, and Christelle Jozet-Alves. 2020. "Cuttlefish Retrieve Whether They Smelt or Saw a Previously Encountered Item." *Scientific Reports* 10:5413. https://doi.org/10.1038/s41598-020-62335-x.

Billard, Pauline, Alexandra K. Schnell, Nicola S. Clayton, and Christelle Jozet-Alves. 2020. “Cuttlefish Show Flexible and Future-Dependent Foraging Cognition.” *Biology Letters* 16 (2): 20190743. https://doi.org/10.1098/rsbl.2019.0743.

Boal, Jean Geary, Andrew W. Dunham, Kevin T. Williams, and Roger T. Hanlon. 2000. Experimental Evidence for Spatial Learning on Octopuses (*Octopus bimaculoides*). *Journal of Comparative Psychology* 114 (3): 246–252. https://doi.org/10.1037/0735-7036.114.3.246.

Boycott, B. B., and J. Z. Young. 1950. “The Comparative Study of Learning.” In *Symposia of the Society for Experimental Biology, No. 4: Physiological Mechanisms in Animal Behavior*, edited by J. F. Danielli and R. Brown. Academic Press.

Boycott, B. B., and J. Z. Young. 1957. “Reversal of Learned Responses in *Octopus vulgaris* Lamarck.” *Animal Behaviour*, 6 (1–2): 45–52. https://doi.org/10.1016/0003-3472(58)90007-1.

Bublitz, Alexander, Guido Dehnhard, and Frederike D. Hanke. 2021. “Reversal of a Spatial Discrimination Task in the Common Octopus (*Octopus vulgaris*).” *Frontiers in Behavioral Neuroscience* 15:614523. https://doi.org/10.3389/fnbeh.2021.614523.

Bublitz, Alexander, Severine R. Weinhold, Sophia Strobel, Guido Dehnhard, and Frederike D. Hanke. 2017. “Reconsideration of Serial Visual Reversal Learning in Octopus (*Octopus vulgaris*) from a Methodological Perspective.” *Frontiers in Physiology* 8:54. https://doi.org/10.3389/fphys.2017.00054.

Cartron, Lelia, Anne-Sophie Darmaillacq, and Ludovic Dickel. 2013. “The Prawn-in-the-Tube Procedure: What Do Cuttlefish Learn and Memorize?” *Behavioural Brain Research*, 240 (1): 29–32. https://doi.org/10.1016/j.bbr.2012.11.010.

Cartron, Lelia, Anne-Sophie Darmaillacq, Christelle Jozet-Alves, Nadav Shashar, and Ludovic Dickel. 2012. “Cuttlefish Rely on Both Polarized Light and Landmarks for Orientation.” *Animal Cognition* 15 (4): 591–596. https://doi.org/10.1007/s10071-012-0487-9.

Chichery, Raymond, and Marie-Paule Chichery. 1992. “Learning Performances and Aging in Cuttlefish (*Sepia officinalis*).” *Experimental Gerontology* 27 (2): 233–239. https://doi.org/10.1016/0531-5565(92)90047-4.

Clayton, Nicola S., Timothy J. Bussey, and Anthony Dickinson. 2003. “Can Animals Recall the Past and Plan for the Future?” *Nature Reviews Neuroscience* 4 (8): 685–91. https://doi.org/10.1038/nrn1180.

Clayton, Nicola S., and Anthony Dickinson. 1998. “Episodic-Like Memory During Cache Recovery by Scrub Jays.” *Nature* 395 (6699): 272–275. https://doi.org/10.1038/26216.

Crook, Robyn J., and Jennifer A. Basil. 2008. “A Biphasic Memory Curve in the Chambered Nautilus, *Nautilus pompilius* L. (Cephalopoda: Nautiloidea).” *Journal of Experimental Biology* 211 (12): 1992–1998. https://doi.org/10.1242/jeb.018531.

Crook, Robyn J., and Jennifer A. Basil. 2012. “Flexible Spatial Orientation and Navigational Strategies in Chambered Nautilus.” *Ethology* 119 (1): 77–85. https://doi.org/10.1111/eth.12040.

Crook, Robyn J., Roger T. Hanlon, and Jennifer A. Basil. 2009. “Memory of Visual and Topographical Features Suggests Spatial Learning in Nautilus (*Nautilus pompilius* L.).” *Journal of Comparative Psychology* 123 (3): 264–274. https://doi.org/10.1037/a0015921.

Crook, Robyn J., Roger T. Hanlon, and Edgar T. Walters. 2013. Squid Have Nociceptors That Display Widespread Long-Term Sensitization and Spontaneous Activity After Bodily Injury.” *Journal of Neuroscience* 33 (24): 10021–10026. https://doi.org/10.1523/jneurosci.0646-13.2013.

Dickel, Ludovic, Marie-Paule Chichery, and Raymond Chichery. 1998. “Time Differences in the Emergence of Short- and Long-Term Memory During Post-Embryonic Development in the Cuttlefish, *Sepia*.” *Behavioural Processes* 44 (1): 81–86. https://doi.org/10.1016/S0376-6357(98)00024-2.

Dufour, Valerie, Claudia A. F. Wascher, Anna Braun, Rachael Miller, and Thomas Bugnyar. 2012. “Corvids Can Decide if Future Exchange is Worth Waiting for.” *Biology Lett*ers 8 (2): 201–204. https://doi.org/10.1098/rsbl.2011.0726.

Forsythe, John W., and Roger T. Hanlon. 1997. “Foraging and Associated Behavior by *Octopus cyanea* Gray, 1849 on a Coral Atoll, French Polynesia.” *Journal of Experimental Marine Biology and Ecology* 209 (1–2): 15–31. https://doi.org/10.1016/S0022-0981(96)00057-3.

Gilly, William. F., and Mary T. Lucero. 1992. “Behavioral Responses to Chemical Stimulation of the Olfactory Organ in the Squid *Loligo opalescens*.” *Journal of Experimental Biology* 162 (1): 209–229. https://doi.org/10.1242/jeb.162.1.209.

Hillemann, Friederike, Thomas Bugnyar, Kurt Kotrschal, and Claudia A. F. Wascher. 2014. “Waiting for Better, Not for More: Corvids Response to Quality in Two Delay Maintenance Tasks.” *Animal Behaviour* 90 (April): 1–10. https://doi.org/10.1016/j.anbehav.2014.01.007.

Hochner, Binyamin, Euan R. Brown, Marina Langella, Tal Shomrat, and Graziano Fiorito. 2003. “A Learning and Memory Area in the Octopus Brain Manifests a Vertebrate-Like Long-Term Potentiation.” *Journal of Neurophysiology* 90 (5): 3547–3554. https://doi.org/10.1152/jn.00645.2003.

Jozet-Alves, Christelle, Marion Bertin, and Nicola S. Clayton. 2013. “Evidence of Episodic-Like Memory in Cuttlefish.” *Current Biology* 23 (23): R1033–R1035. https://doi.org/10.1016/j.cub.2013.10.021.

Karson, Miranda A., Jean Geary Boal, and Roger T. Hanlon. 2003. “Experimental Evidence for Spatial Learning in Cuttlefish (*Sepia officinalis*).” *Journal of Comparative Psychology* 117 (2): 149–155. https://doi.org/10.1037/0735-7036.117.2.149.

Kuba, Michael J., Ruth A. Byrne, Daniela V. Meisel, and Jennifer A. Mather. 2006. “Exploration and Habituation in Intact Free Moving *Octopus vulgaris*.”*International Journal of Comparative Psychology* 19 (4): 426–438. https://doi.org/10.46867/ijcp.2006.19.04.02.

Kuba, Michael J., Letizia Zullo, Ruth A. Byrne, and Binyamin Hochner. 2007. “Visual Habituation in the Common Octopus (*Octopus vulgaris*).” In *Proceedings of the 2nd International Symposium Coleoid Cephalopods Through Time, Prague, 26-29, September 2005*, edited by Martin Košťák and Jaroslav Marek. Acta Universitatis Carolinae. Geologica 49. Charles University.

Kuba, Michael J., Letizia Zullo, and Binyamin Hochner. 2005. “Non Associative Learning in the Common Octopus (*Octopus vulgaris*).” In *2nd International Symposium “Coleoid Cephalopods Through Time,” Prague, September 26-28, 2005: Short Papers/Abstracts*, edited by Martin Košťák and Jaroslav Marek. https://www.researchgate.net/publication/280804542.

Long, Traci M., Roger T. Hanlon, Andries Ter Maat, and Harold M. Pinsker. 1989. “Non-Associative Learning in the Squid *lolliguncula brevis* (Mollusca, Cephalopoda).” *Marine Behaviour and Physiology* 16 (1): 1–9. https://doi.org/10.1080/10236248909378736.

Mackintosh, J. 1962. “An Investigation of Reversal Learning in *Octopus vulgaris* Lamarck.” *Journal of Experimental Psychology* 14 (1): 15–22. https://doi.org/10.1080/17470216208416506.

Mackintosh, N. J., and J. Mackintosh. 1963. “Reversal Learning in *Octopus vulgaris* Lamarck With and Without Irrelevant Cues. *Quarterly Journal of Experimental Psychology* 15 (4): 236–242. https://doi.org/10.1080/17470216308416332.

Mackintosh, N. J., and J. Mackintosh. 1964. “Performance of *Octopus* over a Series of Reversals of a Simultaneous Discrimination.” *Animal Behaviour* 12 (2–3): 321–324. https://doi.org/10.1016/0003-3472(64)90019-3.

Martin-Ordas, Gema, Daniel Haun, Fernando Colmenares, and Josep Call. 2010. “Keeping Track ofTtime: Evidence for Episodic-Like Memory in Great Apes.”*Animal Cognition* 13 (2): 331–340. https://doi.org/10.1007/s10071-009-0282-4.

Mather, Jennifer A. 1991. “Navigation by Spatial Memory and Use of Visual Landmarks in Octopuses.” *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 168 (4): 491–497. https://doi.org/10.1007/BF00199609.

Messenger, John B. 1973a. “Learning in the Cuttlefish, *Sepia*.” *Animal Behaviour* 21 (4): 801–826. https://doi.org/10.1016/S0003-3472(73)80107-1.

Messenger, John B. 1973b. “Learning Performance and Brain Structure: A Study in Development.” *Brain Research* 58 (2): 519–523. https://doi.org/10.1016/0006-8993(73)90025-5.

Nixon, Marion, and J. Z. Young. 2003. *The Brains and Lives of Cephalopods*. Oxford University Press.

Purdy, Jesse E., Deann Dixon, Aleta Estrada, Anne Peters, Elizabeth Riedlinger, and Ryan Suarez. 2006. “Prawn-in-a-Tube Procedure: Habituation or Associative Learning in Cuttlefish?” *The Journal of General Psychology* 133 (2): 131–152. https://doi.org/10.3200/GENP.133.2.131-152.

Poncet, Lisa, Coraline Desnous, Cécile Bellanger, and Christelle Jozet-Alves. 2022. “Unruly Octopuses Are the Rule: *Octopus vulgaris* Use Multiple and Individually Variable Strategies in an Episodic-Memory Task.” *Journal of Experimental Biology*, 225 (19): jeb244234. https://doi.org/10.1242/jeb.244234.

Rosati, Alexandra G., Jeffrey R. Stevens, Brian Hare, and Marc D. Hauser. 2007. “The Evolutionary Origins of Human Patience: Temporal Preferences in Chimpanzees, Bonobos, and Human Adults.” *Current Biology* 17 (19): 1663–1668. https://doi.org/10.1016/j.cub.2007.08.033.

Samson, Julia E., T. Aran Mooney, Sander W. S. Gussekloo, and Roger T. Hanlon. 2014. “Graded Behavioral Responses and Habituation to Sound in the Common Cuttlefish *Sepia officinalis*.” *Journal of Experimental Biology* 217 (24): 4347–4355. https://doi.org/10.1242/jeb.113365.

Schnell, Alexandra K., Markus Boeckle, and Nicola S. Clayton. 2022. “Waiting for a Better Possibility: Delay of Gratification in Corvids and Its Relationships to Other Cognitive Capacities.” In “Thinking About Possibilities: Mechanisms, Ontogeny, Functions and Phylogeny,” edited by Jonathan Redshaw and Patricia A. Ganea. Theme issue, *Philosophical Transactions of the Royal Society B: Biological Sciences* 377 (1866): 20210348. https://doi.org/10.1098/rstb.2021.0348.

Schnell, Alexandra K., Markus Boeckle, Micaela Rivera, Nicola S. Clayton, and Roger T. Hanlon. 2021. “Cuttlefish Exert Self-Control in a Delay of Gratification Task.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1946): 20203161. https://doi.org/10.1098/rspb.2020.3161.

Schnell, Alexandra K., and Nicola S. Clayton. 2022. “Evolutionary Origins of Complex Cognition.” In *Evolution of Learning and Memory Mechanisms*, edited by Mark A. Krause, Karen L. Hollis, and Mauricio R. Papini. Cambridge University Press.

Schnell, Alexandra K., Nicola S. Clayton, Roger T. Hanlon, and Christelle Jozet-Alves. 2021. “Episodic-Like Memory Is Preserved with Age in Cuttlefish.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1957): 20211052. https://doi.org/10.1098/rspb.2021.1052.

Shomrat, Tal, Ilaria Zarrella, Graziano Fiorito, and Binyamin Hochner. 2008. “The Octopus Vertical Lobe Modulates Short-Term Learning Rate and Uses LTP to Acquire Long-Term Memory.” *Current Biology* 18 (5): 337–342. https://doi.org/10.1016/j.cub.2008.01.056.

Sutherland, N. S. 1957a. “Visual Discrimination of Orientation and Shape by the Octopus.” *Nature* 179 (4549): 11–13. https://doi.org/10.1038/179011a0.

Sutherland, N. S. 1957b. “Visual Discrimination of Orientation by Octopus.”*British Journal of Psychology* 48 (1): 55–71. https://doi.org/10.1111/j.2044-8295.1957.tb00599.x.

Sutherland, N. S. 1960. “The Visual Discrimination of Shape by Octopus: Squares and Rectangles.” *Journal of Comparative and Physiological Psychology* 53 (1): 95–103. https://doi.org/10.1037/h0038429.

Sutherland, N. S. 1963. “The Shape-Discrimination of Stationary Shapes by Octopuses.” *American Journal of Psychology* 76 (2): 177–190. https://doi.org/10.2307/1419155.

Sutherland, N. S., J. Mackintosh, and N. J. Mackintosh. 1963. “The Visual Discrimination of Reduplicated Patterns by Octopus.” *Animal Behaviour* 11 (1): 106–110. https://doi.org/10.1016/0003-3472(63)90017-4.

Tulving, Endel. 1983. *Elements of Episodic Memory*. Oxford University Press

Tulving, Endel. 2005. “Episodic Memory and Autoneosis: Uniquely Human?” In *The Missing Link in Cognition: Origins of Self-Reflective Consciousness*, edited by Herbert S. Terrace and Janet Metcalf. Oxford University Press.

Wells, M. J. 1963. “Taste by Touch: Some Experiments with *Octopus*.” *Journal of Experimental Biology* 40 (1): 87–193. https://doi.org/10.1242/jeb.40.1.187.

Wells, M. J. 1964a. “Detour experiments with Octopuses.” *Journal of Experimental Biology* 41 (3): 621–642. https://doi.org/10.1242/jeb.41.3.621.

Wells, M. J. 1964b. “Tactile Discrimination of Surface Curvature and Shape by the Octopus.” *Journal of Experimental Biology* 41 (2): 433–445. https://doi.org/10.1242/jeb.41.2.433.

Wells, M. J. 1968. “Sensitization and the Evolution of Associative Learning”. In *Neurobiology of Invertebrates*, edited by János Salánki. Springer.

Wells, M. J., N. H. Freeman, and M. Ashburner. 1965. “Some Experiments on the Chemotactile Sense of Octopuses.” *Journal of Experimental Biology* 43 (3): 553–563. https://doi.org/10.1242/jeb.43.3.553.

Wells, M. J., and J. Z. Young. 1968. “Learning with Delayed Rewards in Octopus.” *Zeitschrift für vergleichende Physiologie* 61 (1): 103–128. https://doi.org/10.1007/BF00339147.

Young, J. Z. 1961. “Learning and Discrimination in the Octopus.” *Biological Reviews* 36 (1): 32–96. https://doi.org/10.1111/j.1469-185X.1961.tb01432.x.

Young, J. Z. 1962. “Repeated Reversal of Training in Octopus.” *Quarterly Journal of Experimental Psychology* 14 (4): 206–222. https://doi.org/10.1080/17470216208416539.

Young, J. Z. 1965. “The Central Nervous System of *Nautilus*.” *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 249 (754): 1–25. https://doi.org/10.1098/rstb.1965.0006.

Zepeda, Emily A., Robert J. Veline, and Robyn J. Crook. 2017. “Rapid Associative Learning and Stable Long-Term Memory in the Squid *Euprymna scolopes*.” *Biological Bulletin* 232 (3): 212–218. https://doi.org/10.1086/693461.

CHAPTER 5

Sociality and Mating Strategies

Large brains and flexible, intelligent behavior are often thought to be linked to sociality. Yet cephalopods appear to be an exception: for all their well-known intelligence, they are largely non-social. In fact, the capacity for sociality varies among the cephalopods.[1] Some squid species hunt in large shoals,[2] and cuttlefish assemble in large groups at certain times of the year for spawning events.[3] Nonetheless, most octopus species, as well as most deep-water cephalopods such as nautiluses and vampire squid, are presumed to spend most of their lives living in a solitary manner.[4] They have even been described as “antisocial.”[5] Nearly all examples of sociality observed in the cephalopods occur in the context of resource competition and reproductive behavior.

Squid are the most social of cephalopods, in so far as they spend a significant portion of their lives in close proximity with one another in large shoals.[2] In addition to making it easier to find a mate,[6] shoaling behavior can help squid avoid predation by both increasing their chances of detecting a predator[7] and by spreading out the chance of getting caught across many shoal members.[8] It has even been suggested that the coral reef squid (*Sepioteuthis sepioidea*) may exhibit “sentinel” behavior, with one member swimming on the edge of the group to provide an early warning to the rest of the shoal in the case of a nearby predator.[9]

Even though individual squid hunt while in shoals, there is no evidence of *coordinated* hunting among squid. The only definitive case of collaborative hunting in any cephalopod involves collaborations between the big blue octopus, also known as the day octopus (*Octopus cyanea*), and several species of reef fishes. Although either the octopus or the fish can initiate the hunt, the octopuses then coordinate it, using changes to their posture and patterns of movement to cue responses from their hunting partners, who guard the escape routes from a section of reef while the octopus reaches in with their arms to extract the prey.[10]

Male-against-male competition over access to females is present in nearly all studied cephalopods.[11] Other forms of competition between members of the same species have been observed in octopuses. Being mostly confined to the seafloor, octopuses make dens to help them avoid predators. It seems likely that, in at least some octopus species, there is competition over access to good den sites.[12] In most cases, octopuses choose dens further away from other octopuses, all else being equal.[5],[13] However, it can sometimes be the case that the only suitable den spaces in the area are all concentrated in a small space.[14] Sometimes, this seems to lead to a degree of social tolerance. Octopuses probably use various strategies to avoid unnecessary aggression from other octopuses. These strategies include respecting dominance hierarchies[15] and signaling intentions using skin color patterns.[16] In some species, males may choose dens adjacent to particularly favoured females.[14] In the larger Pacific striped octopus, male-female pairs have been observed to cohabit in the same den and even share food.[17]

The most intricate examples of sociality observed in cephalopods center on mating behavior. Male octopuses,[18] cuttlefish,[3] and squid[19],[20] have all been observed to employ mating strategies that vary with body size. In cuttlefish and squid species, larger males compete vigorously with each other via intense displays of skin color patterns,[3] fin beating,[6] and biting[3] to gain access to females. The winning males monopolize the females and try to mate guard them from other males. The smaller males, by contrast, attempt to “sneak” copulations with the guarded females, sometimes utilizing female-specific skin color patterns to slip past the guards undetected (a behavior known as sexual mimicry).[6] Meanwhile, in the algae octopus (*Abdopus aculeatus*), a species in which reproductive adults live in close proximity to each other, larger males choose dens adjacent to large females so that they can guard them from mating with other males.[21] In this species too, smaller males will often use female "solicitation" displays to sneak past the larger males and copulate with guarded females.[18]

Despite the prevalence of dramatic male visual displays in cephalopod mating behavior, the responses of females are usually far more subtle, if they respond at all, leaving the role of visual signaling in cephalopod courtship quite unclear.[11] These visual signals might help females to recognize the sex or species of males,[22] and they may also signal intent. Female rejection of male copulation attempts are rare among squids but common in both cuttlefish[23] and octopuses.[24] In most cases, it is uncertain which male traits influence female receptivity. However, growing evidence strongly suggests that processes after copulation, especially sperm competition and cryptic female choice (that is, processes in the female that alter the chances of fertilization, depending on the male), have a large effect on reproductive outcomes in cephalopods.[11]

An important component of all social behavior of cephalopods is social *recognition*. This is the capacity of individuals in a species to recognize other members of the same species. This may take the form of recognizing them as individuals or placing them in a relevant category (such as female, dominant, etc.). The extent of social recognition, and the mechanisms enabling it, vary substantially among cephalopods.[22] While visual cues are likely to aid many cephalopods in assessing the sex or dominance of another octopus, only one species (the common octopus, *Octopus vulgaris*) has so far been shown to recognize *individuals* by sight.[25] On the whole, cephalopods appear to rely heavily on chemosensing for social recognition (on chemosensing, see the entry on Perceiving the World).[26] Several species have been found to discriminate the sex[27] or mating history[28] of other octopuses from a distance, based on chemical cues in the water.

Additionally, males of several octopus and cuttlefish species are thought to recognize previous mates, or potentially competing male sperm, using chemosensing on contact.[24]

In summary, cephalopods are not particularly social animals outside of reproduction. However, the mating behaviors of cephalopods are complex and can require cognitively demanding tasks, such as memory of prior mates, rapid decision-making, and subtle forms of communication. The evolution of sensory abilities and social recognition appear heavily intertwined with these reproduction-focused social behaviors. This form of sociality should not be overlooked, then, as one of the main evolutionary drivers of cognitive complexity in these highly intelligent animals.

References

1 Ikeda 2009

2 a b Benoit-Bird and Gilly 2012

3 a b c d Hall and Hanlon 2002

4 Hanlon and Messenger 2018

5 a b O'Brien et al. 2021

6 a b c Jantzen and Havenhand 2003

7 Pitcher 1986

8 Parrish 1991

9 Moynihan and Rodaniche 1982

10 Bayley and Rose 2020

11 a b c Morse and Huffard 2019

12 Aronson 1986

13 Edsinger et al. 2020

14 a b Godfrey-Smith and Lawrence 2012

15 Cigliano 1993

16 Scheel et al. 2016

17 Caldwell et al. 2015

18 a b Huffard et al. 2008

19 Wada et al. 2005

20 Hanlon et al. 2002

21 Huffard et al. 2010

22 a b Boal 2006

23 Schnell et al. 2015

24 a b Morse et al. 2015

25 Tricarico et al. 2011

26 Morse and Huffard 2022

27 Morse et al. 2017

28 Boal 1997

Key Texts

Boal, Jean Geary. 2006. "Social Recognition: A Top Down View of Cephalopod Behaviour." In "The Cuttlefish *Sepia officinalis*: A Working Model in Cephalopod Research," edited by Noussithé Koueta, J. Pedro Andrade, and Sigurd von Boletzky. Special issue, *Vie et Milieu / Life and Environment* 56 (2): 69-79.

Social recognition is a necessary prerequisite for cooperative behavior and an important aspect of sociality in all animals. This review summarizes the evidence for and against different forms of social recognition among cephalopods.

Caldwell, Roy L., Richard Ross, Arcadio Rodaniche, and Christine L. Huffard. 2015. "Behavior and Body Patterns of the Larger Pacific Striped Octopus." *PLOS ONE* 10 (8): e0134152. https://doi.org/10.1371/journal.pone.0134152.

This study invesigated the behavior of the larger Pacific striped octopus in the laboratory for the first time, revealing several social behaviors never before seen in any other octopus species.

Edsinger, Eric, Reuven Pnini, Natsumi Ono, Ryoko Yanagisawa, Kathryn Dever, and Jonathan Miller. 2020. "Social Tolerance in *Octopus laqueus*—a Maximum Entropy Model." *PLOS ONE* 15 (6): e0233834. https://doi.org/10.1371/journal.pone.0233834.

This study found evidence that social tolerance varies depending on environmental conditions in octopuses, and can be influenced by external factors such as availability of suitable den spaces.

Hall, Karina C., and Roger T. Hanlon. 2002. "Principal Features of the Mating System of a Large Spawning Aggregation of the Giant Australian Cuttlefish *Sepia apama* (Mollusca: Cephalopoda)." *Marine Biology* 140 (3): 533-545. https://doi.org/10.1007/s00227-001-0718-0.

This detailed analysis outlines the complex reproductive behavior of Australian giant cuttlefish in the field.

Hanlon, Roger T. 1998. "Mating Systems and Sexual Selection in the Squid *Loligo*: How Might Commercial Fishing on Spawning Squids Affect Them?" *California Cooperative Oceanic Fisheries Investigations Report* 39:92–100. https://calcofi.org/downloads/publications/calcofireports/v39/CalCOFI_Rpt_Vol_39_1998.pdf.

This study describes the importance of alternative mating tactics and sperm competition in the reproductive behavior of *Loligo* squid.

Hanlon, Roger T., and John B. Messenger. 2018. *Cephalopod Behaviour*. 2nd ed. Cambridge University Press.

This book provides an expert, authoritative review of all cephalopod behavior to the time of its publication, focusing on social behavior.

Huffard, Christine L. 2007. "Ethogram of *Abdopus aculeatus* (d'Orbigny, 1834) (Cephalopoda: Octopodidae): Can Behavioural Characters Inform Octopodid Taxomony and Systematics?" *Journal of Molluscan Studies* 73 (2): 185–193. https://doi.org/10.1093/mollus/eym015.

This study provides a thorough analysis of behavioral traits in a relatively social octopus species.

Huffard, Christine L., Roy L. Caldwell, and Farnis Boneka. 2008. "Mating Behavior of *Abdopus aculeatus* (d'Orbigny 1834) (Cephalopoda: Octopodidae) in the Wild." *Marine Biology* 154 (2): 353–362. https://doi.org/10.1007/s00227-008-0930-2.

For the first time, this field study found sophisticated reproductive behaviors in octopuses. These were previously only thought to occur within mating assemblages of cuttlefish and squid. Some of these reported behaviors include alternative mating tactics, mating strategies dependent on size, and denning within close proximity to mates.

Ikeda, Yuzuru. 2009. "A Perspective on the Study of Cognition and Sociality of Cephalopod Mollusks, a Group of Intelligent Marine Invertebrates." In "Divergence of Comparative Cognitive Studies in Japan," edited by Shigeru Watanabe. Special issue, *Japanese Psychological Research* 51 (3): 146–153. https://doi.org/10.1111/j.1468-5884.2009.00401.x.

A useful review, providing a summary and comparison of social behavior among the cephalopods.

Jantzen, Troy M., and Jon N. Havenhand. 2003. "Reproductive Behavior in the Squid *Sepioteuthis australis* from South Australia: Interactions on the Spawning Grounds." *Biological Bulletin* 204 (3): 305–317. https://doi.org/10.2307/1543601.

This study details the reproductive behaviors observed in spawning assemblages of *Sepioteuthis* squid.

Morse, Peter, and Christine L. Huffard. 2019. "Tactical Tentacles: New Insights on the Processes of Sexual Selection Among the Cephalopoda." *Frontiers in Physiology* 10:1035. https://doi.org/10.3389/fphys.2019.01035.

This review summarizes and compares the known reproductive behaviors among cephalopods, providing new insights and hypotheses regarding the importance of processes after copulation in the evolution of cephalopod reproductive systems.

Scheel, David, Peter Godfrey-Smith, and Matthew Lawrence. 2016. "Signal Use by Octopuses in Agonistic Interactions." *Current Biology* 26 (3): 377–382. https://doi.org/10.1016/j.cub.2015.12.033.

This study identified that some octopus may manage territorial disputes by signaling intent via different displays of color patterns on the skin.

Tricarico, Elena, Luciana Borrelli, Francesca Gherardi, and Graziano Fiorito. 2011. "I Know My Neighbour: Individual Recognition in *Octopus vulgaris*." *PLOS ONE* 6 (4): e18710. https://doi.org/10.1371/journal.pone.0018710.

For the first time, this study demonstrated that a cephalopod can visually recognize and discriminate among individuals of the same species.

Bibliography

Adamo, Shelley A., William M. Brown, Alison J. King, et al. 2000. "Agonistic and Reproductive Behaviours of the Cuttlefish *Sepia officinalis* in a Semi-Natural Environment." *Journal of Molluscan Studies* 66 (3): 417–419. https://doi.org/10.1093/mollus/66.3.417.

Amodio, Piero, Markus Boeckle, Alexandra K. Schnell, Ljerka Ostojíc, Graziano Fiorito, and Nicola S. Clayton. 2019. "Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence?" *Trends in Ecology and Evolution* 34 (1): 45–56. https://doi.org/10.1016/j.tree.2018.10.010.

Aronson, Richard B. 1986. "Life History and Den Ecology of *Octopus briareus* Robson in a Marine Lake." *Journal of Experimental Marine Biology and Ecology* 95 (1): 37–56. https://doi.org/10.1016/0022-0981(86)90086-9.

Bayley, D. T. I., and A. Rose. 2020. "Multi-Species Co-Operative Hunting Behaviour in a Remote Indian Ocean Reef System." *Marine and Freshwater Behaviour and Physiology* 53 (1): 35–42. https://doi.org/10.1080/10236244.2020.1746658.

Benoit-Bird, Kelly J., and William F. Gilly. 2012. "Coordinated Nocturnal Behavior of Foraging Jumbo Squid *Dosidicus gigas*." *Marine Ecology Progress Series* 455:211–228. https://doi.org/10.3354/meps09664.

Boal, Jean Geary. 1997. "Female Choice of Males in Cuttlefish (Mollusca: Cephalopoda)." *Behaviour* 134 (13–14): 975–988. https://doi.org/10.1163/156853997X00340.

Boal, Jean Geary. 2006. "Social Recognition: A Top Down View of Cephalopod Behaviour." In "The Cuttlefish *Sepia officinalis*: A Working Model in Cephalopod Research," edited by Noussithé Koueta, J. Pedro Andrade, and Sigurd von Boletzky. Special issue, *Vie et Milieu / Life and Environment* 56 (2): 69–79.

Boal, Jean Geary, and D. K. Golden. 1999. "Distance Chemoreception in the Common Cuttlefish, *Sepia officinalis* (Mollusca, Cephalopoda)." *Journal of Experimental Marine Biology and Ecology* 235 (2): 307–317. https://doi.org/10.1016/S0022-0981(98)00187-7.

Buresch, Kendra C., Jean Geary Boal, Jamie Knowles, et al. 2003. "Contact Chemosensory Cues in Egg Bundles Elicit Male-Male Agonistic Conflicts in the Squid *Loligo pealei* (Mollusca: Cephalopoda)." *Journal of Chemical Ecology* 29 (3): 547–560. https://doi.org/10.1023/A:1022846603591.

Bush, Stephanie L., Hendrik J. T. Hoving, Christine L. Huffard, Bruce H. Robison, and Louis D. Zeidberg. 2012. "Brooding and Sperm Storage by the Deep-Sea Squid *Bathyteuthis berryi* (Cephalopoda: Decapodiformes)." *Journal of the Marine Biological Association of the United Kingdom* 92 (7): 1629–1636. https://doi.org/10.1017/S0025315411002165.

Caldwell, Roy L., Richard Ross, Arcadio F. Rodaniche, and Christine L. Huffard. 2015. “Behavior and Body Patterns of the Larger Pacific Striped Octopus.” *PLOS ONE* 10 (8): e0134152. https://doi.org/10.1371/journal.pone.0134152.

Cigliano, John A. 1993. “Dominance and Den Use in *Octopus bimaculoides*.” *Animal Behaviour* 46 (4): 677–684. https://doi.org/10.1006/anbe.1993.1244.

Cigliano, John A. 1995. “Assessment of the Mating History of Female Pygmy Octopuses and a Possible Sperm Competition Mechanism.” *Animal Behaviour* 49 (3): 849–851. https://doi.org/10.1016/0003-3472(95)80218-5.

Colgan, Patrick W. 1983. *Comparative Social Recognition*. Wiley.

Corner, Barbara D., and Howard T. Moore. 1981. “Field Observations on Reproductive Behavior of *Sepia latimanus*.” *Micronesica* 16 (2): 235–260. https://micronesica.org/sites/default/files/corner_b.d._moore_h.t.-field_observations_on_the_reproductive_behavior_of_sepia_latimanus-micronesica_vol.16_no.2_dec._19800.pdf.

Edsinger, Eric, Reuven Pnini, Natsumi Ono, Ryoko Yanagisawa, Kathryn Dever, and Jonathan Miller. 2020. “Social Tolerance in *Octopus laqueus*—a Maximum Entropy Model.” *PLOS ONE* 15 (6): e0233834. https://doi.org/10.1371/journal.pone.0233834.

Godfrey-Smith, Peter, and Matthew Lawrence. 2012. “Long-Term High-Density Occupation of a Site by *Octopus tetricus* and Possible Site Modification Due to Foraging Behavior.” *Marine and Freshwater Behaviour and Physiology* 45 (4): 1–8. https://doi.org/10.1080/10236244.2012.727617.

Hall, Karina C., and Roger T. Hanlon. 2002. “Principal Features of the Mating System of a Large Spawning Aggregation of the Giant Australian Cuttlefish *Sepia apama* (Mollusca: Cephalopoda).” *Marine Biology* 140 (3): 533–545. https://doi.org/10.1007/s00227-001-0718-0.

Hanlon, Roger T. 1998. “Mating Systems and Sexual Selection in the Squid *Loligo*: How Might Commercial Fishing on Spawning Squids Affect Them?” *California Cooperative Oceanic Fisheries Investigations Report* 39:92–100. https://calcofi.org/downloads/publications/calcofireports/v39/CalCOFI_Rpt_Vol_39_1998.pdf.

Hanlon, Roger T., S. A. Ament, and Howaida R. Gabr. 1999. “Behavioral Aspects of Sperm Competition in Cuttlefish, *Sepia officinalis* (Sepioidea: Cephalopoda).” *Marine Biology* 134 (4): 719–728. https://doi.org/10.1007/s002270050588.

Hanlon, Roger T., Michael R. Maxwell, and Nadav Shashar. 1997. “Behavioral Dynamics That Would Lead to Multiple Paternity within Egg Capsules of the Squid *Loligo pealei*.” *Biological Bulletin* 193 (2): 212–214. https://doi.org/10.1086/bblv193n2p212.

Hanlon, Roger T., and John B. Messenger. 2018. *Cephalopod Behaviour*. 2nd ed. Cambridge University Press.

Hanlon, Roger T., Malcolm J. Smale, and Warwick H. H. Sauer. 1994. "An Ethogram of Body Patterning Behavior in the Squid *Loligo vulgaris reynaudii* on Spawning Grounds in South Africa." *Biological Bulletin* 187 (3): 363–372. https://doi.org/10.2307/1542293.

Hanlon, Roger T., Malcolm J. Smale, and Warwick H. H. Sauer. 2002. "The Mating System of the Squid *Loligo vulgaris reynaudii* (Cephalopoda, Mollusca) off South Africa: Fighting, Guarding, Sneaking, Mating and Egg Laying Behavior." *Bulletin of Marine Science* 71 (1): 331–345. https://www.ingentaconnect.com/contentone/umrsmas/bullmar/2002/00000071/00000001/art00025.

Hoving, Hendrik Jan T., Marek R. Lipinski, John J. Videler, and Kat S. R. Bolstad. 2010. "Sperm Storage and Mating in the Deep-Sea Squid *Taningia danae* Joubin, 1931 (Oegopsida: Octopoteuthidae)." *Marine Biology* 157 (2): 393–400. https://doi.org/10.1007/s00227-009-1326-7.

Huffard, Christine L. 2005. "The Behavioural Ecology and Locomotion of *Abdopus aculeatus* (d'Orbigny, 1834)." PhD diss., University of California, Berkeley. https://doi.org/10.13140/RG.2.1.3489.8960.

Huffard, Christine L. 2007. "Ethogram of *Abdopus aculeatus* (d'Orbigny, 1834) (Cephalopoda: Octopodidae): Can Behavioural Characters Inform Octopodid Taxomony and Systematics?" *Journal of Molluscan Studies* 73 (2): 185–193. https://doi.org/10.1093/mollus/eym015.

Huffard, Christine L., Roy L. Caldwell, and Farnis Boneka. 2008. "Mating Behavior of *Abdopus aculeatus* (d'Orbigny 1834) (Cephalopoda: Octopodidae) in the Wild." *Marine Biology* 154 (2): 353–362. https://doi.org/10.1007/s00227-008-0930-2.

Huffard, Christine L., Roy L. Caldwell, and Farnis Boneka 2010. "Male-Male and male-Female Aggression May Influence Mating Associations in Wild Octopuses (*Abdopus aculeatus*)." *Journal of Comparative Psychology* 124 (1): 38–46. https://doi.org/10.1037/a0017230.

Ikeda, Yuzuru. 2009. "A Perspective on the Study of Cognition and Sociality of Cephalopod Mollusks, a Group of Intelligent Marine Invertebrates." In "Divergence of Comparative Cognitive Studies in Japan," edited by Shigeru Watanabe. Special issue, *Japanese Psychological Research* 51 (3): 146–153. https://doi.org/10.1111/j.1468-5884.2009.00401.x.

Jantzen, Troy M., and Jon N. Havenhand. 2003. "Reproductive Behavior in the Squid *Sepioteuthis australis* from South Australia: Interactions on the Spawning Grounds." *Biological Bulletin* 204 (3): 305–317. https://doi.org/10.2307/1543601.

Mäthger, Lydia M., and Roger T. Hanlon. 2007. "Malleable Skin Coloration in Cephalopods: Selective Reflectance, Transmission and Absorbance of Light by Xhromatophores and Iridophores." *Cell and Tissue Research* 329 (1): 179–186. https://doi.org/10.1007/s00441-007-0384-8.

Mäthger, Lydia M., Nadav Shashar, and Roger T. Hanlon. 2009. "Do Cephalopods Communicate Using Polarized Light Reflections from Their Skin?" *Journal of Experimental Biology* 212 (14): 2133–2140. https://doi.org/10.1242/jeb.020800.

Mohanty, Sobhi, Alfredo F. Ojanguren, and Lee A. Fuiman. 2014. "Aggressive Male Mating Behavior Depends on Female Maturity in *Octopus bimaculoides*." *Marine Biology* 161 (7): 1521–1530. https://doi.org/10.1007/s00227-014-2437-3.

Morse, Peter. 2008. "Female Mating Preference Polyandry and Paternity Bias in *Octopus tetricus*." Honours thesis, The University of Western Australia. http://doi.org/10.13140/RG.2.1.4113.6084

Morse, Peter, and Christine L. Huffard. 2019. "Tactical Tentacles: New Insights on the Processes of Sexual Selection Among the Cephalopoda." *Frontiers in Physiology* 10:1035. https://doi.org/10.3389/fphys.2019.01035.

Morse, Peter, and Christine L. Huffard. 2022. "Chemotactile Social Recognition in the Blue-Ringed Octopus, *Hapalochlaena maculosa*." *Marine Biology* 169 (8): 99. https://doi.org/10.1007/s00227-022-04087-y.

Morse, Peter, Kyall R. Zenger, Mark I. McCormick, Mark G. Meekan, and Christine L. Huffard. 2015. "Nocturnal Mating Behaviour and Dynamic Male Investment of Copulation Time in the Southern Blue-Ringed Octopus, *Hapalochlaena maculosa* (Cephalopoda: Octopodidae)." *Behaviour* 152 (14): 1883–1910. https://doi.org/10.1163/1568539X-00003321.

Morse, Peter, Kyall R. Zenger, Mark I. McCormick, Mark G. Meekan, and Christine L. Huffard. 2017. "Chemical Cues Correlate with Agonistic Behaviour and Female Mate Choice in the Southern Blue-Ringed Octopus, *Hapalochlaena maculosa* (Hoyle, 1883) (Cephalopoda: Octopodidae)." *Journal of Molluscan Studies* 83 (1): 79–87. https://doi.org/10.1093/mollus/eyw045.

Moynihan, Martin, and Arcadio F. Rodaniche. 1982. "The Behavior and Natural History of the Caribbean Reef Squid *Sepioteuthis sepioidea* with a Consideration of Social, Signal, and Defensive Patterns for Difficult and Dangerous Environments." *Fortschritte der Verhaltensforschung* 25:9–150.

Norman, Mark D., Julian Finn, and Tom Tregenza. 1999. "Female Impersonation as an Alternative Reproductive Strategy in Giant Cuttlefish." *Proceedings of the Royal Society B: Biological Sciences.* 266 (1426): 1347–1349. https://doi.org/10.1098/rspb.1999.0786.

O'Brien, Duncan A., Michelle L. Taylor, Heather D. Masonjones, Philipp H. Boersch-Supan, and Owen R. O'Shea. 2021. "An Experimental Assessment of Social Tolerance and Den Ecology in a High-Density Octopus Population." *Marine Biology* 168 (5): 61. https://doi.org/10.1007/s00227-021-03865-4.

Parrish, Julia K. 1991. "Do Predators 'Shape' Fish Schools: Interactions Between Predators and Their Schooling Prey." *Netherlands Journal of Zoology* 42 (2–3): 358–370. https://doi.org/10.1163/156854291X00388.

Perez, José Angel Alvarez, Manuel Haimovici, and João Carlos Brahm Cousin. 1990. “Sperm Storage Mechanism and Fertilization in Females of Two South American Eledonids (Cephalopoda: Octopoda).” *Malacologia* 32 (1): 147–154.

Pitcher, Tony J. 1986. “Functions of Shoaling Behaviour in Teleosts.” In *The Behaviour of Teleost Fishes*, edited by Tony J. Pitcher. Chapman and Hall.

Plotnik, Joshua M., and Nicola S. Clayton. 2015. “Convergent Cognitive Evolution Across Animal Taxa: Comparisons of Chimpanzees, Corvids, and Elephants.” In *The Conceptual Mind: New Directions in the Study of Concepts*, edited by Eric Margolis and Stephen Laurence. MIT Press.

Rocha, Francisco, Ángel Guerra, and Ángel F. González. 2001. “A Review of Reproductive Strategies in Cephalopods.” *Biological Reviews* 76 (3): 291–304. https://doi.org/10.1017/S1464793101005681.

Sauer, Warwick H. H., Mike J. Roberts, Marek R. Lipinski, et al. 1997. “Choreography of the Squid’s ‘Nuptial Dance.’” *Biological Bulletin* 192 (2): 203–207. https://doi.org/10.2307/1542714.

Scheel, David, Peter Godfrey-Smith, and Matthew Lawrence. 2016. “Signal Use by Octopuses in Agonistic Interactions.” *Current Biology* 26 (3): 377–382. https://doi.org/10.1016/j.cub.2015.12.033.

Schnell, Alexandra K., Carolynn L. Smith, Roger T. Hanlon, and Robert T. Harcourt. 2015. “Female Receptivity, Mating History, and Familiarity Influence the Mating Behavior of Cuttlefish.” *Behavioral Ecology and Sociobiology* 69 (2): 283–292. https://doi.org/10.1007/s00265-014-1841-5.

Shigeno, Shuichi, Paul L. R. Andrews, Giovanna Ponte, and Graziano Fiorito. 2018. “Cephalopod Brains: An Overview of Current Knowledge to Facilitate Comparison With Vertebrates.” *Frontiers in Physiology* 9:952. https://doi.org/10.3389/fphys.2018.00952.

Tricarico, Elena, Luciana Borrelli, Francesca Gherardi, and Graziano Fiorito. 2011. “I Know My Neighbour: Individual Recognition in *Octopus vulgaris*.” *PLOS ONE* 6 (4): e18710. https://doi.org/10.1371/journal.pone.0018710.

van Schaik, Carel P., and Judith M. Burkart. 2011. “Social Learning and Evolution: The Cultural Intelligence Hypothesis.” In “Culture Evolves,” edited by Andrew Whiten, Robert A. Hinde, Christopher B. Stringer, and Kevin N. Laland. Discussion meeting issue, *Philosophical Transactions of the Royal Society B: Biological Sciences* 366 (1567): 1008–1016. https://doi.org/10.1098/rstb.2010.0304.

Voight, Janet R. 1991. “Ligula Length and Courtship in *Octopus digueti*: A Potential Mechanism of Mate Choice.” *Evolution* 45 (7): 1726–1730. https://doi.org/10.1111/j.1558-5646.1991.tb02680.x.

Wada, Toshifumi, Takeshi Takegaki, Tohru Mori, and Yutaka Natsukari. 2005. “Alternative Male Mating Behaviors Dependent on Relative Body Size in Captive Oval Squid *Sepioteuthis lessoniana* (Cephalopoda, Loliginidae).” *Zoological Science* 22 (6): 645–651. https://doi.org/10.2108/zsj.22.645.

Wada, Toshifumi, Takeshi Takegaki, Tohru Mori, and Yutaka Natsukari. 2010. “Sperm Removal, Ejaculation and Their Behavioural Interaction in Male Cuttlefish in Response to Female Mating History.” *Animal Behaviour* 79 (3): 613–619. https://doi.org/10.1016/j.anbehav.2009.12.004.

Walderon, Matthew D., Kevin J. Nolt, Robert E. Haas, et al. 2011. “Distance Chemoreception and the Detection of Conspecifics in *Octopus bimaculoides*.” *Journal of Molluscan Studies* 77 (3): 309–311. https://doi.org/10.1093/mollus/eyr009.

Wells, M. J., and J. Wells. 1972. “Sexual Displays and Mating of *Octopus vulgaris* Cuvier and *O. cyanea* Gray and Attempts to Alter Performance by Manipulating the Glandular Condition of the Animals.” *Animal Behaviour* 20 (2): 293–308. https://doi.org/10.1016/S0003-3472(72)80051-4.

CHAPTER 6

Navigating the Environment

The need to meet higher energy demands, and to do it without the protection of an outer shell, drove the soft-bodied cephalopods to evolve adaptations that allow them to hunt prey with ruthless effectiveness—and to find safety before falling prey themselves to other predators.[1] To achieve this, they use a variety of efficient strategies, taking full advantage of their advanced sensory abilities and impressive capacity for learning and thinking about the spatial environment. To survive, they must locate and remember food sources,[2],[3] find their way back to shelter or home territories,[4] and to remember the location of other members of their species.[5]

Most other molluscs (e.g. snails) rely on a muscular "foot" for moving around. In the cephalopods, this foot has been modified into a siphon (a structure that expels water) and a muscular set of arms.[6] Their movement relies on concerted contractions of various muscle groups around a hydrostatic skeleton: a structure of fluid-filled muscle that can be continually reshaped, allowing limbs to become temporarily rigid or flexible as needed.[6] To imagine approximately what this is like, think of your tongue or an elephant's trunk. Cephalopods vary in their specific movement styles, depending on the extent to which their shell has been reduced or eliminated by evolution.

In the nautiloids, the outer shell provides protection, reducing the need for speed and maneuverability. They can adjust their buoyancy within the water column by regulating the ratio of air and water within different chambers of their shell, and navigate with short bursts of jet propulsion by expelling water through their siphon.[7] By contrast, squid (Myopsida and Oegopsida) have adopted a much more aerodynamic body plan, reducing their shells to all but an internal, cartilaginous pen for musculature support. Through undulating fin movements and jet propulsion, squids use speed and agility to evade predators.[8] Cuttlefish (Sepiida) have similar locomotory movements to squids. They possess a flattened, calcareous cuttlebone that assists in regulating buoyancy. This internal shell limits their speed and agility relative to squid. They rely instead on crypsis (a general term for camouflage and concealment) to elude predation.[9] Octopuses (Octopoda) have lost the shell altogether. Most species move around their environments through push and pull movements using their eight arms and suckers, a strategy made possible by living on the seabed.[6] They sometimes walk on two or more arms, as well as using forward and backward jet propulsion (like cuttlefish and squid). The absence of hard body structures, apart from the beak, enables octopuses to fit into incredibly tight spaces in order to hide from their predators. Additionally, some deep-sea cephalopods, which live in environments with potentially fewer food sources or predatory pressures, employ powered-swimming using their fins[10] or "medusoid" swimming using the webbing between their arms.[11]

Having advanced eyes and visual acuity (see "Perceiving the World"),[12] cephalopods have long been thought to rely on visual cues or landmarks for short-distance navigation. However, tests involving mazes suggest that some species remember sequences of past movements (such as a pattern of left or right turns from a given starting position) to help them orient themselves in their environment.[13] Cuttlefish have been observed to navigate based on the plane of polarization of the ambient light. This may help them navigate in turbid or deep waters where other visual cues are limited.[14]

Chemosensation is undoubtedly very important for cephalopods.[15] However, investigations of its role in navigation (chemotaxis) have been limited. Two species of octopus (the East Pacific red octopus, *Octopus rubescens*, and the giant Pacific octopus, *Enteroctopus dofleini*) are known to respond to odor plumes while foraging for food.[3] Additionally, cephalopods possess two ways of registering changes in pressure: the lateral line system and statocysts.[16] It is possible that these organs might assist some cephalopods to detect their position in the water column, facilitating navigation of a three-dimensional environment.

So far, investigations of cephalopod navigation in the wild have focused on octopuses and cuttlefish. They display strong tendencies to return to particular sites ("site-fidelity"), while searching for prey and mates over extremely large areas away from their dens.[17] One individual Pacific giant octopus (*E. dofleini*) was observed to use an average space of over 50,000 m^2 per foraging trip, apparently navigating by following contours within their environment.[17] Meanwhile, a study of foraging behavior in the big blue octopus, *Octopus cyanea*, observed this species to strike out elaborate hunting paths while out hunting for prey and to then head directly back to the den once finished, suggesting spatial knowledge of the surrounding area.[4] Similar behavior has also been observed in at least two other octopus species (*Octopus vulgaris* and *Octopus rubescens*).[18],[19]

There is a particular region of the brain of soft-bodied cephalopods—*the vertical lobe complex*—that is thought to be of special significance for learning and remembering the spatial structure of the environment. It is often said to be somewhat analogous to the *hippocampus* in the brains of vertebrates.[20] One plausible hypothesis is that soft-bodied cephalopods have two kinds of spatial memory: "working spatial memory" that they use when exploring *new* environments, and "reference spatial memory" that they use for home areas that are likely to remain constant over time.[8] There is also evidence in cuttlefish of "episodic-like memory": remembering facts about what happened, where, and when to inform decisions while searching for prey. For more detail on this, see "Learning and Memory."[2]

During spatial learning tasks, cuttlefish have been observed to prefer vertical visual cues over horizontal cues when discriminating between two-dimensional targets, highlighting the special importance of *vertical* information for cephalopods as they navigate their three-dimensional ocean environments.[21] Interestingly, adult male cuttlefish travel longer distances when exploring new environments and rely more heavily on visual cues when solving spatial tasks than females or juveniles.[22] These findings suggest sexual dimorphism of spatial cognition in this species. This may have arisen because male cuttlefish need to explore larger territories in order to maximize potential mates.[22]

Nautiloids lack a vertical lobe and have fewer neurons overall than their soft-bodied cousins. Yet they have been observed to learn spatial information relatively quickly within a laboratory setting and to retain this information for at least two weeks.[23] These are intriguing findings, suggesting that further research on nautiloids, and more detailed comparisons between nautiloids and other cephalopods, would be worthwhile.

References

1 Leite et al. 2009

2 a b Jozet-Alves et al. 2013

3 a b Weertman 2022

4 a b Forsythe and Hanlon 1997

5 Huffard et al. 2008

6 a b c Alupay and Mather 2017

7 Chamberlain (1987) 2010

8 a b Alves et al. 2008

9 Hanlon and Messenger 1988

10 Vecchione and Young 1997

11 Seibel et al. 1998

12 Hanke and Kelber 2020

13 Alves et al. 2007

14 Cartron et al. 2012

15 Morse and Huffard 2022

16 Budelmann 1996

17 a b Scheel and Bisson 2012

18 Mather 1991a

19 Mather 1991b

20 Shomrat et al. 2015

21 Scatà et al. 2016

22 a b Jozet-Alves et al. 2008

23 Crook et al. 2009

Key Texts

Alupay, Jean, and Jennifer A. Mather. 2017. “Locomotion of Coleoid Cephalopods.” In *Physiology of Molluscs: A Collection of Selected Reviews*, vol. 1, edited by Saber Saleuddin and Spencer Mukai. Apple Academic Press.

A comprehensive review of the evolution of different locomotory strategies among cephalopods.

Alves, Christelle, Jean Geary Boal, and Ludovic Dickel. 2008. “Short-Distance Navigation in Cephalopods: A Review and Synthesis.” In “Spatial Navigation,” edited by Demis Basso. Special issue, *Cognitive Processing* 9 (4): 239–247. https://doi.org/10.1007/s10339-007-0192-9.

A review of the current evidence, both in the field and laboratory, of cephalopod navigational strategies.

Crook, Robyn J., Roger T. Hanlon, and Jennifer A. Basil. 2009. “Memory of Visual and Topographical Features Suggests Spatial Learning in Nautilus (*Nautilus pompilius* L.).” *Journal of Comparative Psychology* 123 (3): 264–274. https://doi.org/10.1037/a0015921.

This research investigated spatial learning in nautiloids for the first time. Contrary to earlier assumptions, the researchers discovered that nautiloids have spatial learning capacities comparable to soft-bodied cephalopods.

Forsythe, John W., and Roger T. Hanlon. 1997. “Foraging and Associated Behavior by *Octopus cyanea* Gray, 1849 on a Coral Atoll, French Polynesia.” *Journal of Experimental Marine Biology and Ecology* 209 (1–2): 15–31. https://doi.org/10.1016/S0022-0981(96)00057-3.

This was one of the first field studies to find evidence for advanced navigational abilities in octopuses.

Leite, Tatiana Silva, Manuel Haimovici, and Jennifer A. Mather. 2009. “*Octopus insularis* (Octopodidae), Evidences of a Specialized Predator and a Time-Minimizing Hunter.” *Marine Biology* 156 (11): 2355-2367. https://doi.org/10.1007/s00227-009-1264-4.

This was one of the first pieces of research to propose that octopuses rely on specialized navigational abilities to help them minimize exposure to potential predators.

Mather, Jennifer A. 1991b. “Navigation by Spatial Memory and Use of Visual Landmarks in Octopuses.” *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 168 (4): 491–497. https://doi.org/10.1007/BF00199609.

This laboratory study analyzed the use of visual cues in octopus navigation and found evidence that octopuses are always aware of exactly how far they are from their dens, even when out of sight.

Scatà, Gabriella, Christelle Jozet-Alves, Céline Thomasse, Noam Josef, and Nadav Shashar. 2016. “Spatial Learning in the Cuttlefish *Sepia officinalis*: Preference for Vertical over Horizontal Information.” *Journal of Experimental Biology* 219 (18): 2928–2933. https://doi.org/10.1242/jeb.129080.

This laboratory study was one of the first to investigate spatial learning in cuttlefish.

Bibliography

Aitken, J. P, Ron K. O'Dor, and George D. Jackson. 2005. "The Secret Life of the Giant Australian Cuttlefish *Sepia apama* (Cephalopoda): Behaviour and Energetics in Nature Revealed Through Radio Acoustic Positioning and Telemetry (RAPT)." *Journal of Experimental Marine Biology and Ecology* 320 (1): 77–91. https://doi.org/10.1016/j.jembe.2004.12.040.

Alupay, Jean, and Jennifer A. Mather. 2017. "Locomotion of Coleoid Cephalopods." In *Physiology of Molluscs: A Collection of Selected Reviews*, vol. 1, edited by Saber Saleuddin and Spencer Mukai. Apple Academic Press.

Alves, Christelle, Jean Geary Boal, and Ludovic Dickel. 2008. "Short-Distance Navigation in Cephalopods: A Review and Synthesis." In "Spatial Navigation," edited by Demis Basso. Special issue, *Cognitive Processing* 9 (4): 239–247. https://doi.org/10.1007/s10339-007-0192-9.

Alves, Christelle, Raymond Chichery, Jean Geary Boal, and Ludovic Dickel. 2007. "Orientation in the Cuttlefish *Sepia officinalis*: Response Versus Place Learning." *Animal Cognition* 10 (1): 29–36. https://doi.org/10.1007/s10071-006-0027-6.

Boal, Jean Geary, K. M. Wittenberg, and Roger T. Hanlon. 2000. "Observational Learning Does Not Explain Improvement in Predation Tactics by Cuttlefish (Mollusca: Cephalopoda)." *Behavioural Processes* 52 (2–3): 141–153. https://doi.org/10.1016/S0376-6357(00)00137-6.

Boal, Jean Geary, and D. K. Golden. 1999. "Distance Chemoreception in the Common Cuttlefish, *Sepia officinalis* (Mollusca, Cephalopoda)." *Journal of Experimental Marine Biology and Ecology* 235 (2): 307–317. https://doi.org/10.1016/S0022-0981(98)00187-7.

Budelmann, Bernd U. 1996. "Active Marine Predators: The Sensory World of Cephalopods." *Marine and Freshwater Behaviour and Physiology* 27 (2–3): 59–75. https://doi.org/10.1080/10236249609378955.

Cartron, Lelia, Anne-Sophie Darmaillacq, Christelle Jozet-Alves, Nadav Shashar, and Ludovic Dickel. 2012. "Cuttlefish Rely on Both Polarized Light and Landmarks for Orientation." *Animal Cognition* 15 (4): 591–596. https://doi.org/10.1007/s10071-012-0487-9.

Chamberlain, John A., Jr. (1987) 2010. "Locomotion of *Nautilus*." In *Nautilus: The Biology and Paleobiology of a Living Fossil*, edited by W. Bruce Saunders and Neil H. Landman. Topics in Geobiology, vol 6. Springer.

Crook, Robyn J., Roger T. Hanlon, and Jennifer A. Basil. 2009. "Memory of Visual and Topographical Features Suggests Spatial Learning in Nautilus (*Nautilus pompilius* L.)." *Journal of Comparative Psychology* 123 (3): 264–274. https://doi.org/10.1037/a0015921.

Di Cosmo, Anna, and Gianluca Polese. 2017. "Cephalopod Olfaction." *Oxford Research Encyclopedia of Neuroscience*, July 27. https://doi.org/10.1093/acrefore/9780190264086.013.185.

Forsythe, John W., and Roger T. Hanlon. 1997. "Foraging and Associated Behavior by *Octopus cyanea* Gray, 1849 on a Coral Atoll, French Polynesia." *Journal of Experimental Marine Biology and Ecology* 209 (1–2): 15–31. https://doi.org/10.1016/S0022-0981(96)00057-3.

Hanke, Frederike D., and Almut Kelber. 2020. "The Eye of the Common Octopus (*Octopus vulgaris*)." *Frontiers in Physiology* 10:1637. https://doi.org/10.3389/fphys.2019.01637.

Hanlon, Roger T., and John B. Messenger. 1988. "Adaptive Coloration in Young Cuttlefish (*Sepia officinalis* L.): The Morphology and Development of Body Patterns and Their Relation to Behaviour." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 320 (1200): 437–487. https://doi.org/10.1098/rstb.1988.0087.

Huffard, Christine L., Roy L. Caldwell, and Farnis Boneka. 2008. "Mating Behavior of *Abdopus aculeatus* (d'Orbigny 1834) (Cephalopoda: Octopodidae) in the Wild." *Marine Biology* 154 (2): 353–362. https://doi.org/10.1007/s00227-008-0930-2.

Ivey, Gayla L. 2007. "Acoustic Telemetry of the Short-Term Movements of *Octopus cyanea* (Gray, 1849) in Kaneohe Bay, Hawai'i." Master's thesis, University of Hawaii at Manoa. http://hdl.handle.net/10125/20927.

Jozet-Alves, Christelle, Marion Bertin, and Nicola S. Clayton. 2013. "Evidence of Episodic-Like Memory in Cuttlefish." *Current Biology* 23 (23): R1033–R1035. https://doi.org/10.1016/j.cub.2013.10.021.

Jozet-Alves, Christelle, Julien Modéran, and Ludovic Dickel. 2008. "Sex Differences in Spatial Cognition in an Invertebrate: The Cuttlefish." *Proceedings of the Royal Society B: Biological Sciences* 275 (1646): 2049–2054. https://doi.org/10.1098/rspb.2008.0501.

Leite, Tatiana Silva, Manuel Haimovici, and Jennifer A. Mather. 2009. "*Octopus insularis* (Octopodidae), Evidences of a Specialized Predator and a Time-Minimizing Hunter." *Marine Biology* 156 (11): 2355–2367. https://doi.org/10.1007/s00227-009-1264-4.

Mather, Jennifer A. 1991a. "Foraging, Feeding and Prey Remains in Middens of Juvenile *Octopus vulgaris* (Mollusca: Cephalopoda)." *Journal of Zoology* 224 (1): 27–39. https://doi.org/10.1111/j.1469-7998.1991.tb04786.x.

Mather, Jennifer A. 1991b. "Navigation by Spatial Memory and Use of Visual Landmarks in Octopuses." *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 168 (4): 491–497. https://doi.org/10.1007/BF00199609.

Morse, Peter, and Christine L. Huffard. 2022. “Chemotactile Social Recognition in the Blue-Ringed Octopus, *Hapalochlaena maculosa*.” *Marine Biology* 169 (8): 99. https://doi.org/10.1007/s00227-022-04087-y.

Polese, Gianluca, Carla Bertapelle, and Anna Di Cosmo. 2015. “Role of Olfaction in *Octopus vulgaris* Reproduction.” *General and Comparative Endocrinology* 210:55–62. https://doi.org/10.1016/j.ygcen.2014.10.006.

Restle, Frank. 1957. “Discrimination of Cues in Mazes: A Resolution of the ‘Place-vs.-Response’ Question.” *Psychological Review* 64 (4): 217–228. https://doi.org/10.1037/h0040678.

Saunders, W. Bruce, and Neil H. Landman, eds. 2010. *Nautilus: The Biology and Paleobiology of a Living Fossil*. Topics in Geobiology, vol 6. Springer.

Scatà, Gabriella, Christelle Jozet-Alves, Céline Thomasse, Noam Josef, and Nadav Shashar. 2016. “Spatial Learning in the Cuttlefish *Sepia officinalis*: Preference for Vertical over Horizontal Information.” *Journal of Experimental Biology* 219 (18): 2928–2933. https://doi.org/10.1242/jeb.129080.

Scheel, David, and L. Bisson. 2012. “Movement Patterns of Giant Pacific Octopuses, *Enteroctopus dofleini* (Wülker, 1910).” *Journal of Experimental Marine Biology and Ecology* 416–417:21–31. https://doi.org/10.1016/j.jembe.2012.02.004.

Scheel, David, A. Lauster, and T. L. S. Vincent. 2007. “Habitat Ecology of *Enteroctopus dofleini* from Middens and Live Prey Surveys in Prince William Sound, Alaska.” In *Cephalopods Present and Past: New Insights and Fresh Perspectives*, edited by Neil H. Landman, Richard Arnold Davis, and Royal H. Mapes. Springer.

Schnell, Alexandra K., Nicola S. Clayton, Roger T. Hanlon, and Christelle Jozet-Alves. 2021. “Episodic-Like Memory is Preserved with Age in Cuttlefish.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1957): 20211052. https://doi.org/10.1098/rspb.2021.1052.

Seibel, Brad A., Erik V. Thuesen, and James J. Childress. 1998. “Flight of the Vampire: Ontogenetic Gait-Transition in *Vampyroteuthis infernalis* (Cephalopoda: Vampyromorpha).” *Journal of Experimental Biology* 201 (16): 2413–2424. https://doi.org/10.1242/jeb.201.16.2413.

Shomrat, Tal, Ana Turchetti-Maia, N. Stern-Mentch, Jennifer A. Basil, and Binyamin Hochner. 2015. “The Vertical Lobe of Cephalopods: An Attractive Brain Structure for Understanding the Evolution of Advanced Learning and Memory Systems.” In Invertebrate Neuroscience” edited by Alison R. Mercer and Bing Zhang. Special issue, *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology A* 201 (9): 947–956. https://doi.org/10.1007/s00359-015-1023-6.

Vecchione, Michael, and Richard E. Young. 1997. “Aspects of the Functional Morphology of Cirrate Octopods: Locomotion and Feeding.” *Vie et milieu / Life and Environment* 47 (2): 101–110. https://wwwphp.obs-banyuls.fr/Viemilieu/images/Archives_1950-2002/vie-et-milieu/VOLUME_1997_47_fasc2.pdf.

Walderon, Matthew D., Kevin J. Nolt, Robert E. Haas, et al. 2011. “Distance Chemoreception and the Detection of Conspecifics in *Octopus bimaculoides*.” *Journal of Molluscan Studies* 77 (3): 309–311. https://doi.org/10.1093/mollus/eyr009.

Weertman, Willem Lee. 2022. “Octopus Use Odor Plumes to Find Food.” Masters thesis, Alaska Pacific University. https://www.proquest.com/dissertations-theses/octopus-use-odor-plumes-find-food/docview/2760559049/se-2.

Young, J. Z. 1991. “Computation in the Learning System of Cephalopods.” *Biological Bulletin* 180 (2): 200–208. https://doi.org/10.2307/1542389.

Young, Richard E., Michael Vecchione, and D. T. Donovan. 1998. “The Evolution of Coleoid Cephalopods and Their Present Biodiversity and Ecology.” *South African Journal of Marine Science* 20 (1): 393–420. https://doi.org/10.2989/025776198784126287.

CHAPTER 7

Self-Regulation and Self-Awareness

In studies of animal minds, researchers define self-regulation or self-control as the ability to *hold back* from seizing a less valuable reward, waiting (or, sometimes, investing greater effort) to attain a more valuable reward.[1],[2] By exploring the self-control abilities of other animals, we can gain a better understanding of how they make decisions and think about the future.

How do researchers study self-control? A common approach is to use "delayed gratification" tasks, which test the animal's ability to wait for a tastier (or larger) reward, even when they have to forego an immediate reward to get it (Figure 16).[3] Self-control abilities have been found in several primates,[4] rodents,[5] birds,[5],[6],[7] and fish[8] using these tasks. But what about cephalopods?

In 2021, Alexandra Schnell and colleagues used a delayed gratification task to test common cuttlefish (*Sepia officinalis*).[9] The researchers gave the cuttlefish a choice between a less desirable but immediately accessible prey item and a more desirable prey item that (as the cuttlefish knew from prior training) could sometimes be accessed after a delay, provided they avoided the immediate reward. Cuttlefish tended to avoid the immediate reward and waited up to 50–130 seconds to obtain the more valuable reward: clear evidence of self-control.

Intriguingly, the individuals that could sustain longer delays in the task also outperformed the others also in a follow-up experiment which tested other learning abilities. Just as in chimpanzees,[10] this points to a link between self-control abilities and general cognitive ability. However, future research is needed to investigate this link.

Before this study, there were already some emerging signs of self-control in cephalopods. Both the common octopus (*Octopus vulgaris*) and common cuttlefish can learn to hold back from predatory attacks when the prey is able to hurt them (for example, when crabs have stinging sea anemones on their backs[11]) or when the prey is inside a container.[12], [13]

This “inhibitory control”—the ability to hold back from executing an instinctive behavior or reflex response—is likely to be very important to the predation strategies used by cephalopods, especially “ambush feeding.”[14] When hunting highly mobile animals like fishes and shrimps, the ability to wait for the right moment is crucial. Cephalopods need to hold back their attack until their prey has moved into a vulnerable position from which it can be grabbed. In other kinds of animal, such as birds and fishes, performance in inhibitory control tasks has been found to be linked to the size of integrative brain regions[15],[16] and to success in survival and reproduction,[17] hinting that this need to flexibly override instincts and reflexes may be a crucial driver of the evolution of large, complex brains. The same links may well exist in cephalopods too, but this has not yet been studied.

Self-*awareness* is the ability to become the object of one’s own attention.[18],[19] This ability comes in degrees: some animals are more or less self-aware than others, and in more or less sophisticated ways. This is an important dimension of variation in the conscious lives of animals.[20] The “mirror-mark test,”[21] also known as the “mirror test” or the “mark test” is the most influential test for assessing self-awareness in other species. The test uses *mirror self-recognition* (MSR)—the capacity to identify a reflected mirror image as oneself—as an indicator of self-awareness. Animals are first marked with a colored dye on a part of the body that they can only see in a mirror. They are then confronted with their reflections. To pass the test, they must exhibit *mark-directed responses* (such as visual inspection and attempting to remove the mark). They must show these responses only in front of the mirror and only towards visible marks.

So far, evidence of mirror self-recognition has been found only in chimpanzees (the original test subjects), orangutans,[22] elephants,[23] dolphins,[24] magpies[25] (although an attempt to replicate this result failed[26]) and, remarkably, the cleaner wrasse, a small tropical fish.[27] In all cases, this evidence has been the subject of intense debate and controversy. Is the mirror-mark test a good indicator of self-recognition? Is self-recognition a good indicator of self-awareness? There have long been high-profile sceptics.[28],[29],[30] In recent years, a growing number of researchers has been advocating for a more gradualist and nuanced approach to studying self-awareness, allowing for many intermediate degrees between having no self-awareness at all and possessing a concept of self.[19],[20],[31],[32] On this view, rather than asking whether a concept of self is present or absent in non-human animals, researchers should be asking to what *extent* other species are self-aware, using a variety of different experiments to investigate this. Some recent experiments have investigated much more basic forms of self-awareness, such as being aware of one's body parts and their position and movement in space ("body-awareness"[33]).

What about self-awareness in cephalopods? Cephalopods' responses to mirrors have been explored in a few species with mixed results. In one experiment, some octopuses (*Octopus laqueus*, *Hapalochlaena lunulata*, and *Abdopus aculeatus*) did not alter their behavior at all in the presence of a mirror.[34] Yet in another experiment, the common octopus (*Octopus vulgaris*) engaged in extensive physical exploration of the mirror and exhibited various agonistic (aggressive or defensive) responses, apparently directed at the animal in the mirror.[35] Similar types of social behaviors have been observed in cuttlefish and reef squid (*S. officinalis*, *S. pharaonic*, *Sepioteuthis lessoniana*[34],[35],[36],[37]). What has never been unequivocally observed in cephalopods is any use of a mirror to inspect parts of the body that cannot be seen directly. These self-exploratory behaviors would be a clear sign of self-recognition but have not been reported for any cephalopods.[38]

Are there any signs of responsiveness to marks on the body seen in the mirror, a key part of the mirror-mark test? Yuzuru Ikeda has reported that, in an unpublished study, reef squids marked with visible dyes did not exhibit mark-directed behaviors, yet showed a stronger tendency to interact with their reflections, relative to invisibly-marked animals with access to the same mirrors.[39] This would be tantalizingly close to evidence of self-recognition. But since the data have not been published, we cannot have high confidence in these claims.

Meanwhile, common octopuses were observed grooming and attempting to remove marks, typically using a single arm.[35] However, these mark-directed responses were exhibited even when the mirror was *not* present, and by invisibly-marked individuals. This suggests that octopuses were feeling the marks on their skin, not responding to their image in the mirror. This highlights a major challenge for experimental researchers: given the incredibly sensitive skin of these animals, is it even possible to mark them without them feeling it? The mirror-mark test was, after all, originally designed for animals with fur. There is need for new ways of assessing self-awareness in cephalopods.

The idea of testing for body awareness, already mentioned earlier, suggests a promising direction for the future. In the octopus nervous system, the limbs have a degree of autonomy from the central brain.[40] Moreover, body parts are not directly represented in the central brain.[41] It seems likely, given this, that the mechanisms supporting the recognition of one's own body parts in cephalopods may differ substantially from those of vertebrates. There are clearly self-recognition mechanisms of at least a simple kind, since one arm of an octopus can recognize another arm of the same animal and refrain from interfering with it, treating it differently from the arm of another octopus.[42] But there is much we do not understand about how bodily self-recognition works in cephalopods. Studying body awareness could be a crucial step toward assessing cephalopods' ability to be aware of themselves.

References

1 Del Giudice 2015

2 Beran 2015

3 Miller et al. 2019

4 Beran et al. 1999

5 a b Green et al. 2004

6 Dufour et al. 2012

7 Auersperg et al., 2013

8 Aellen et al. 2021

9 Schnell et al. 2021

10 Beran and Hopkins 2018

11 Ross 1971

12 Agin et al. 2006

13 Borrelli et al. 2020

14 Hanlon and Messenger 2018

15 MacLean et al. 2014

16 Trik et al. 2023

17 Ashton et al. 2018

18 Morin 2006

19 a b Lage et al. 2022

20 a b Birch et al. 2020

21 Gallup 1970

22 Suarez and Gallup 1981

23 Plotnik et al. 2006

24 Reiss and Marino 2001

25 Prior et al. 2008

26 Soler et al. 2020

27 Kohda et al. 2019

28 Heyes 1994

29 Heyes 1995

30 Mitchell 1997

31 de Waal 2019

32 Wittek et al. 2021

33 Dale and Plotnik 2017

34 a b Ikeda and Matsumoto 2007

35 a b c Amodio and Fiorito 2022

36 Palmer et al. 2006

37 Ikeda and Matsumura 2008

38 Anderson and Gallup 2015

39 Ikeda 2009

40 Sumbre et al. 2001

41 Zullo et al. 2009

42 Nesher et al. 2014

Key Texts

Amodio, Piero, and Graziano Fiorito. 2022. “A Preliminary Attempt to Investigate Mirror Self-Recognition in *Octopus vulgaris*.” *Frontiers in Physiology* 13:951808. https://doi.org/10.3389/fphys.2022.951808.

This study provides valuable data about the way in which common octopuses perceive and respond to mirrors as well as to relevant control stimuli (non-reflective panels and same-sex conspecifics).

Birch, Jonathan, Alexandra K. Schnell, and Nicola S. Clayton. 2020. “Dimensions of Animal Consciousness.” *Trends in Cognitive Sciences* 24 (10): 789–801. https://doi.org/10.1016/j.tics.2020.07.007.

A multidimensional and nuanced framework to study consciousness in non-human animals.

Gallup, Gordon G., Jr. 1970. “Chimpanzees: Self-Recognition.” *Science* 167 (3914): 86–87. https://doi.org/10.1126/science.167.3914.86.

This study used, for the first time, the mirror-mark test to investigate self-awareness in non-human species, providing evidence that chimpanzees are capable of mirror self-recognition.

Ikeda, Yuzuru. 2009. “A Perspective on the Study of Cognition and Sociality of Cephalopod Mollusks, a Group of Intelligent Marine Invertebrates.” In “Divergence of Comparative Cognitive Studies in Japan,” edited by Shigeru Watanabe. Special issue, *Japanese Psychological Research* 51 (3): 146–153. https://doi.org/10.1111/j.1468-5884.2009.00401.x.

This review discusses mirror-induced responses in several species of cephalopods.

Ross, D. M. 1971. “Protection of Hermit Crabs (*Dardanus* spp.) from Octopus by Commensal Sea Anemones (*Calliactis* spp.).” *Nature* 230 (5283): 401–402. https://doi.org/10.1038/230401a0.

This study shows that octopuses can learn to inhibit predatory attacks when the prey is potentially able to hurt them (in this case, stinging anemones were attached to the shells of hermit crabs).

Schnell, Alexandra K., Markus Boeckle, Micaela Rivera, Nicola S. Clayton, and Roger T. Hanlon. 2021. “Cuttlefish Exert Self-Control in a Delay of Gratification Task.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1946): 20203161. https://doi.org/10.1098/rspb.2020.3161.

This groundbreaking study demonstrates temporal delayed gratification in an invertebrate, with waiting times comparable to those observed in certain apes and corvids. Furthermore, it established the initial connection between self-control and intelligence beyond the primate lineage.

Bibliography

Aellen, Mélisande, Valérie Dufour, and Redouan Bshary. 2021. "Cleaner Fish and Other Wrasse Match Primates in Their Ability to Delay Gratification." *Animal Behaviour* 176 (June): 125–143. https://doi.org/10.1016/j.anbehav.2021.04.002.

Agin, Véronique, Raymond Chichery, Ludovic Dickel, and Marie-Paule Chichery. 2006. "The Prawn-in-the-Tube Procedure in Cuttlefish: Habituation or Passive Avoidance Learning?" *Learning and Memory* 13 (1): 97–101. https://doi.org/10.1101/lm.90106.

Amodio, Piero, and Graziano Fiorito. 2022. "A Preliminary Attempt to Investigate Mirror Self-Recognition in *Octopus vulgaris*." *Frontiers in Physiology* 13:951808. https://doi.org/10.3389/fphys.2022.951808.

Anderson, James R., and Gordon G. Gallup Jr. 2015. "Mirror Self-Recognition: A Review and Critique of Attempts to Promote and Engineer Self-Recognition in Primates."*Primates* 56 (4): 317–326. https://doi.org/10.1007/s10329-015-0488-9.

Ashton, Benjamin J., Amanda R. Ridley, Emily K. Edwards, and Alex Thornton. 2018. "Cognitive Performance is Linked to Group Size and Affects Fitness in Australian Magpies." *Nature* 554 (7692): 364–367. https://doi.org/10.1038/nature25503.

Auersperg, A. M. I., I. B. Laumer, and Thomas Bugnyar. 2013. "Goffin Cockatoos Wait for Qualitative and Quantitative Gain but Prefer 'Better' to 'More.'" *Biology Letters* 9 (3): 20121092. https://doi.org/10.1098/rsbl.2012.1092.

Barlow, J. J., and G. D. Sanders. 1974. "Intertrial Interval and Passive Avoidance Learning in *Octopus vulgaris*." *Animal Learning & Behavior* 2 (2): 86–88. https://doi.org/10.3758/BF03199127.

Beran, Michael J. 2015. "The Comparative Science of 'Self-Control': What Are We talking About?" *Frontiers in Psychology* 6:51. https://doi.org/10.3389/fpsyg.2015.00051.

Beran, Michael J, and William D. Hopkins. 2018. "Self-Control in Chimpanzees Relates to General Intelligence." *Current Biology* 28 (4): 574–579.e3. https://doi.org/10.1016/j.cub.2017.12.043.

Beran, Michael J., E. Sue Savage-Rumbaugh, James L. Pate, and Duane M. Rumbaugh. 1999. "Delay of Gratification in Chimpanzees (*Pan troglodytes*)." *Developmental Psychobiology* 34 (2): 119–127. https://doi.org/10.1002/(SICI)1098-2302(199903)34:2%3C119::AID-DEV5%3E3.0.CO;2-P.

Birch, Jonathan, Alexandra K. Schnell, and Nicola S. Clayton. 2020. "Dimensions of Animal Consciousness." *Trends in Cognitive Sciences* 24 (10): 789–801. https://doi.org/10.1016/j.tics.2020.07.007.

Borrelli, Luciana, Cinzia Chiandetti, and Graziano Fiorito. 2020. "A Standardized Battery of Tests to Measure *Octopus vulgaris*' Behavioural Performance." *Invertebrate Neuroscience* 20 (1): 4. https://doi.org/10.1007/s10158-020-0237-7.

Dale, Rachel, and Joshua M. Plotnik. 2017. "Elephants Know When Their Bodies are Obstacles to Success in a Novel Transfer Task." *Scientific Reports* 7:46309. https://doi.org/10.1038/srep46309.

de Waal, Frans B. M. 2019. "Fish, Mirrors, and a Gradualist Perspective on Self-Awareness." *PLOS Biology* 17 (2): e3000112. https://doi.org/10.1371/journal.pbio.3000112.

Del Giudice, Marco. 2015. "Self-Regulation in an Evolutionary Perspective." In *Handbook of Biobehavioral Approaches to Self-Regulation*, edited by Guido H. E. Gendolla, Mattie Tops, and Sander L. Koole. Springer.

Diamond, Adele. 2013. "Executive Functions." *Annual Review of Psychology* 64:135–168. https://doi.org/10.1146/annurev-psych-113011-143750.

Dufour, Valerie, Claudia A. F. Wascher, Anna Braun, Rachael Miller, and Thomas Bugnyar. 2012. "Corvids Can Decide if Future Exchange is Worth Waiting for." *Biology Lett*ers 8 (2): 201–204. https://doi.org/10.1098/rsbl.2011.0726.

Gallup, Gordon G., Jr. 1970. "Chimpanzees: Self-Recognition." *Science* 167 (3914): 86–87. https://doi.org/10.1126/science.167.3914.86.

Green, Leonard, Joel Myerson, Daniel D. Holt, John R. Slevin, and Sara J. Estle. 2004. "Discounting of Delayed Food Rewards in Pigeons and Rats: Is There a Magnitude Effect?" *Journal of the Experimental Analysis of Behavior* 81 (1): 39–50. https://doi.org/10.1901/jeab.2004.81-39.

Hanlon, Roger T., and John B. Messenger. 2018. *Cephalopod Behaviour*. 2nd ed. Cambridge University Press.

Heyes, C. M. 1994. "Reflections on Self-Recognition in Primates." *Animal Behaviour* 47 (4): 909–919. https://doi.org/10.1006/anbe.1994.1123.

Heyes, C. M. 1995. "Self-Recognition in Primates: Further Reflections Create a Hall of Mirrors." *Animal Behaviour* 50 (6): 1533–1542. https://doi.org/10.1016/0003-3472(95)80009-3.

Ikeda, Yuzuru. 2009. "A Perspective on the Study of Cognition and Sociality of Cephalopod Mollusks, a Group of Intelligent Marine Invertebrates." In "Divergence of Comparative Cognitive Studies in Japan," edited by Shigeru Watanabe. Special issue, *Japanese Psychological Research* 51 (3): 146–153. https://doi.org/10.1111/j.1468-5884.2009.00401.x.

Ikeda, Yuzuru, and Gen Matsumoto. 2007. "Mirror Image Reactions in the Oval Squid *Sepioteuthis lessoniana*." *Fisheries Science* 73 (6): 1401–1403. https://doi.org/10.1111/j.1444-2906.2007.01485.x.

Ikeda, Yuzuru, and M. Matsumura. 2008. “Comparison of Reactions to Mirror Among Eight Tropical Cephalopods.” Paper presented at the 27th Annual Meeting of the Japan Ethological Society, Kanazawa, Japan, September 24–26.

Kohda, Masanori, Takashi Hotta, Tomohiro Takeyama, et al. 2019. “If a Fish Can Pass the Mark Test, What Are the Implications for Consciousness and Self-Awareness Testing in Animals?” *PLOS Biology* 17 (2): e3000021. https://doi.org/10.1371/journal.pbio.3000021.

Lage, Caio A., De Wet Wolmarans, and Daniel C. Mograbi. 2022. “An Evolutionary View of Self-Awareness.” *Behavioural Processes* 194 (January): 104543. https://doi.org/10.1016/j.beproc.2021.104543.

MacLean, Evan L., Brian Hare, Charles L. Nunn, et al. 2014. “The Evolution of Self-Control.” *Proceedings of the National Academy of Sciences* 111 (20): E2140–2148. https://doi.org/10.1073/pnas.1323533111.

Miller, Rachael, Markus Boeckle, Sarah A. Jelbert, Anna Frohnwieser, Claudia A. F. Wascher, and Nicola S. Clayton. 2019. “Self-Control in Crows, Parrots and Nonhuman Primates.” *Wiley Interdisciplinary Reviews: Cognitive Science* 10 (6): e1504. https://doi.org/10.1002/wcs.1504.

Mitchell, Robert W. 1997. “Kinesthetic-Visual Matching and the Self-Concept as Explanations of Mirror-Self-Recognition.” *Journal for the Theory of Social Behaviour* 27 (1): 17–39. https://doi.org/10.1111/1468-5914.00024.

Morin, Alain. 2006. “Levels of Consciousness and Self-Awareness: A Comparison and Integration of Various Neurocognitive Views.” *Consciousness and Cognition* 15 (2): 358–371. https://doi.org/10.1016/j.concog.2005.09.006.

Nesher, Nir, Guy Levy, Frank W. Grasso, and Binyamin Hochner. 2014. “Self-Recognition Mechanism Between Skin and Suckers Prevents Octopus Arms from Interfering with Each Other.” *Current Biology* 24 (11): 1271–1275. https://doi.org/10.1016/j.cub.2014.04.024.

Palmer, M. E., M. Richard Calvé, and Shelley A. Adamo. 2006. “Response of Female Cuttlefish *Sepia officinalis* (Cephalopoda) to Mirrors and Conspecifics: Evidence for Signaling in Female Cuttlefish.” *Animal Cognition* 9 (2): 151–155. https://doi.org/10.1007/s10071-005-0009-0.

Plotnik, Joshua M., Frans B. M. de Waal, and Diana Reiss. 2006. “Self-Recognition in an Asian Elephant.” *Proceedings of the National Academy of Sciences* 103 (45): 17053–17057. https://doi.org/10.1073/pnas.0608062103.

Prior, Helmut, Ariane Schwarz, and Onur Güntürkün. 2008. “Mirror-Induced Behavior in the Magpie (*Pica pica*): Evidence of Self-Recognition.” *PLOS Biology* 6 (8): e202. https://doi.org/10.1371/journal.pbio.0060202.

Reiss, Diana, and Lori Marino. 2001. “Mirror Self-Recognition in the Bottlenose Dolphin: A Case of Cognitive Convergence.” *Proceedings of the National Academy of Sciences* 98 (10): 5937–5942. https://doi.org/10.1073/pnas.101086398.

Ross, D. M. 1971. “Protection of Hermit Crabs (*Dardanus* spp.) from Octopus by Commensal Sea Anemones (*Calliactis* spp.).” *Nature* 230 (5283): 401–402. https://doi.org/10.1038/230401a0.

Schnell, Alexandra K., Markus Boeckle, Micaela Rivera, Nicola S. Clayton, and Roger T. Hanlon. 2021. “Cuttlefish Exert Self-Control in a Delay of Gratification Task.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1946): 20203161. https://doi.org/10.1098/rspb.2020.3161.

Soler, Manuel, José Manuel Colmenero, Tomás Pérez-Contreras, and Juan Manuel Peralta-Sánchez. 2020. “Replication of the Mirror Mark Test Experiment in the Magpie (*Pica pica*) Does Not Provide Evidence of Self-Recognition.” *Journal of Comparative Psychology* 134 (4): 363–371. https://doi.org/10.1037/com0000223.

Suarez, Susan D., and Gordon G. Gallup Jr. 1981. “Self-Recognition in Chimpanzees and Orangutans, but Not Gorillas.” *Journal of Human Evolutio*n 10 (2): 175–188. https://doi.org/10.1016/S0047-2484(81)80016-4.

Sumbre, German, Yoram Gutfreund, Graziano Fiorito, Tamar Flash, and Binyamin Hochner. 2001. “Control of Octopus Arm Extension by a Peripheral Motor Program.” *Science* 293 (5536): 1845–1848. https://doi.org/10.1126/science.1060976.

Triki, Zegni, Stephanie Fong, Mirjam Amcoff, Sebastian Vàsquez-Nilsson, and Niclas Kolm. 2023. “Experimental Expansion of Relative Telencephalon Size Improves the Main Executive Function Abilities in Guppy.” *PNAS Nexus* 2 (6): pgad129. https://doi.org/10.1093/pnasnexus/pgad129.

Wittek, Neslihan, Hiroshi Matsui, Nicole Kessel, Fatma Oeksuez, Onur Güntürkün, and Patrick Anselme. 2021. “Mirror Self-Recognition in Pigeons: Beyond the Pass-or-Fail Criterion.” *Frontiers in Psychology* 12:669039. https://doi.org/10.3389/fpsyg.2021.669039.

Zullo, Letizia, German Sumbre, Claudio Agnisola, Tamar Flash, and Binyamin Hochner. 2009. “Nonsomatotopic Organization of the Higher Motor Centers in Octopus.” *Current Biology* 19 (19): 1632–1636. https://doi.org/10.1016/j.cub.2009.07.067.

CHAPTER 8

Emotion

Emotions are rapid, fleeting reactions to environmental circumstances. They are typically categorized into two main types: positive emotions, such as feelings of joy, warmth, pleasure, comfort, and excitement; and negative emotions, such as feelings of distress, anxiety, boredom, fear, and pain. For more detail on pain, see the next entry, "Pain."

Emotions do not just involve outward behavioral responses: they also involve inner, subjective experiences.[1] This can make attributions of emotion to other animals controversial. Clearly, we cannot simply ask other animals how they feel. But we can use a variety of non-verbal methods to investigate the behavioral, neurological, and cognitive aspects of emotion, and this can provide some insight into what the state might feel like to the animal, even though the evidence will not be conclusive. Researchers who are cautious about attributing conscious experiences to other animals sometimes use the term "emotion-like state" to refer to a state that functions in a similar way to an emotion but may or may not involve the conscious element. Researchers have investigated both positive and negative emotions (or emotion-like states) in cephalopods.

Negative Emotions

Research on cephalopod emotions has centered on their ability to experience negative, aversive reactions because these types of emotions raise the most ethical concern. There is strong evidence for a form of pain in octopus, cuttlefish, and squid, but this entry will focus on other emotions.

Evidence of other negative emotions can be gleaned from the way animals react to unpleasant practices or situations. A fair amount of work has investigated the causes of stress in cephalopods. For instance, several species of octopus show signs of stress after being caught in trawl nets, including compromised immune systems.[2] Exposure to unsuitable temperatures or salt concentrations leads to cephalopods exhibiting visual signs of stress and discomfort, such as skin blanching and excessive inking.[3] Cuttlefish presented with an approaching predator on an iPad screen appear to exhibit a form of fear, responding by freezing, compressing their mantle (i.e., body), reducing ventilation rates, and concealing any type of movement.[4] Lack of shelter in captive environments can also evoke fear responses in cephalopods (in the form of rapid retreat and high-speed jetting), sometimes leading to a lasting depression-like state and withdrawal from eating.[5] Cuttlefish frequently display indications of stress in poor captive environments, including erratic swimming patterns, loss of appetite, and behaviors reminiscent of depression such as reduced activity levels, decreased interest in usual activities, and altered responses to rewards.[6]

Octopuses kept in unfavorable environments can exhibit “autophagy,” a type of cannibalism where an animal eats part of itself.[7] This behavior can occur in all octopus species. It was traditionally thought to be caused by stress, but there is now a debate about this, with some suggesting that an infectious pathogen causes this behavior,[8] and others arguing that autophagy is caused by a number of factors. Crowded environments can also increase stress in octopus and cuttlefish, leading to decreased time spent resting and feeding.[9]

Less is known about negative emotions (beyond pain) in squid and nautilus. However, this gap reflects a lack of evidence, not evidence of absence. Future research should prioritize developing methods that effectively examine negative emotions beyond pain. Modifying experimental techniques used for pain assessment could reveal more nuanced insights into negative emotions such as stress, fear, and boredom.

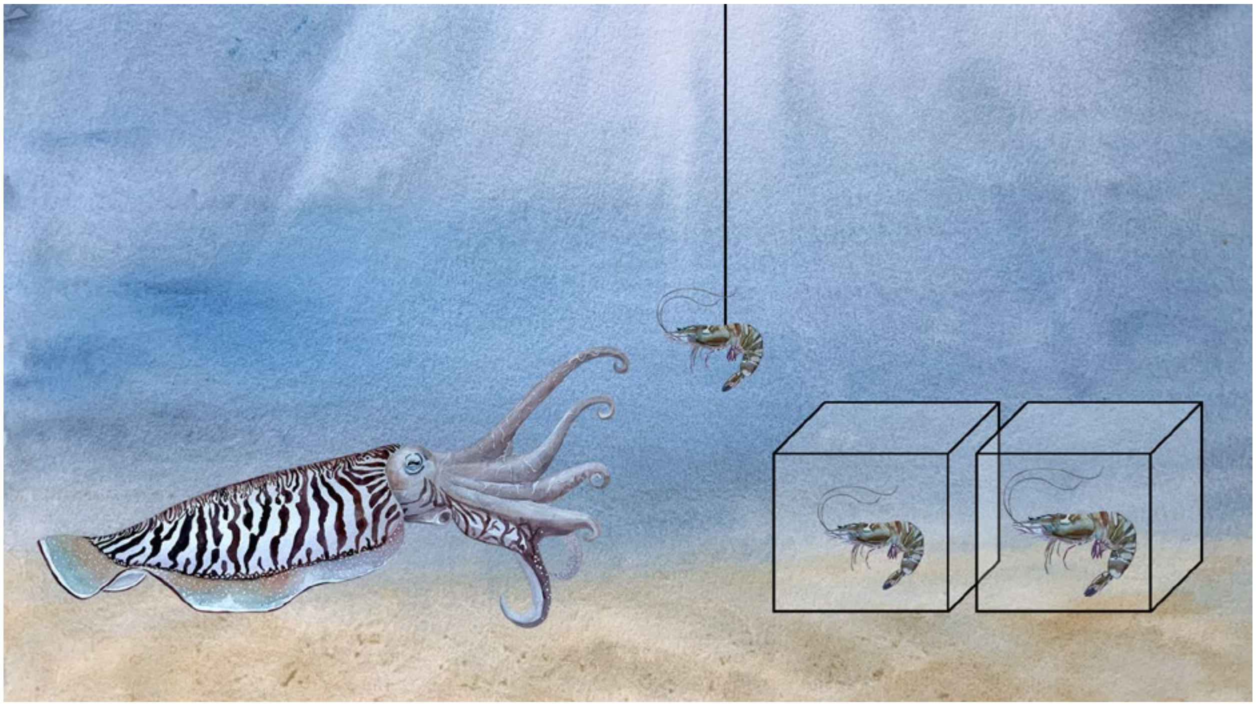

FIGURE 17. Illustration of the experimental set-up in Chung et al., "The Effect of Unexpected Reward on Decision-Making in Cuttlefish." Cuttlefish were presented with a dual-chamber scenario featuring shrimps of varying sizes, aiming to assess their foraging choices. Just prior to this choice, cuttlefish encountered an unexpected reward—a small shrimp—to assess the impact of a surprising event on their decision-making process.

Positive Emotions

Positive emotions in cephalopods are even less explored than negative emotions. One study has explored how cuttlefish react to unexpected rewards.[10] In this study, cuttlefish were presented with an unexpected food reward to assess whether a welcome surprising event would alter their decision-making later, when they were presented with a choice between two food items (i.e., a large shrimp vs. a small shrimp) (Figure 17). The result was that, when cuttlefish received an unexpected food reward, they were quicker to make foraging decisions later. Moreover, they became less discerning: their preference for larger shrimp was reduced. Interestingly, though, the cuttlefish became less discerning even if they didn't actually *eat* the unexpected reward. This suggests it is not the act of eating unexpected food rewards that alters subsequent decisions.

Merely having tried to capture them, regardless of the outcome, is enough to alter their decision-making further down the line. This pattern of behavior does not have any obvious interpretation in terms of positive emotions, but it may provide a useful platform for future work.

Although the question of positive emotions in cephalopods has received very little investigation with experimental methods, there are various behaviors observed in the wild and in captivity that are at least suggestive of positive emotional states. These behaviors include exploration, interaction with novel objects or enrichments, and forms of apparently playful engagement. For example, cuttlefish can use their siphons to spray water at their keeper when they are eager to be fed.[11] Can this behavior be classified as a type of play? This is highly uncertain: there are various possible explanations for such behavior. Meanwhile, octopuses display a keen interest in investigating inanimate plastic objects (i.e., balls, bottles, Lego), towing them around their environment, and passing the items between their arms.[12],[13] Octopuses have also been observed engaging with floating objects by using jets of water, sending the objects to the far end of their tank. They then repeat this action once the object returns, propelled by the incoming current from the aquarium water.[14] The question of whether octopuses experience positive emotions during these play-like activities remains a topic of ongoing investigation. While such actions might suggest experiences of curiosity, enjoyment, or similar positive emotions observed in other animals, it’s important to acknowledge that our understanding of positive emotions in cephalopods is still developing and needs further research.

References

1 Paul et al. 2020

2 Barragán-Méndez et al. 2019

3 Fiorito et al. 2015

4 Bedore et al. 2015

5 Sherrill et al. 2000

6 McDonald 2011

7 Hayter 2005

8 Budelmann 1998

9 Cooke et al. 2019

10 Chung et al. 2022

11 Zylinksi 2015

12 Kuba et al. 2003

13 Kuba et al. 2006

14 Mather and Anderson 1999

Key Texts

Chung, Tzu-Ting, Anne-Sophie Darmaillacq, Ludovic Dickel, and Chuan-Chin Chiao. 2022. "The Effect of Unexpected Reward on Decision-Making in Cuttlefish." *Scientific Reports* 12:2514. https://doi.org/10.1038/s41598-022-06443-w.

This study shows that cuttlefish adjust their foraging strategies in response to previously encountered "surprise" events. Exposure to surprise events appears to trigger an internal emotional-like state in cuttlefish.

Fiorito, Graziano, Andrea Affuso, Jennifer A. Basil, et al. 2015. "Guidelines for the Care and Welfare of Cephalopods in Research—a Consensus Based on an Initiative by CephRes, FELASA and the Boyd Group." *Laboratory Animals* 49 (S2): 1–90. https://doi.org/10.1177/0023677215580006.

This initiative led to guidelines for the care of cephalopod molluscs in research. In the European Union, United Kingdom, Canada, Switzerland, Norway, and parts of Australia, animal welfare law requires humane treatment of cephalopods used in scientific research.

Bibliography

Anderson, David J., and Ralph Adolphs. 2014. “A Framework for Studying Emotions Across Species.” *Cell* 157 (1): 187–200. https://doi.org/10.1016/j.cell.2014.03.003.

Barragán-Méndez, Cristina, Ignacio Sobrino, Adrián Marín-Rincón, et al. 2019. “Acute-Stress Biomarkers in Three Octopodidae Species After Bottom Trawling.” *Frontiers in Physiology* 10:784. https://doi.org/10.3389/fphys.2019.00784.

Barrett, Lisa Feldman, Batja Mesquita, Kevin N. Ochsner, and James J. Gross. 2007. “The Experience of Emotion.” *Annual Review of Psychology* 58:373–403. https://doi.org/10.1146/annurev.psych.58.110405.085709.

Bedore, Christine N., Stephen M. Kajiura, and Sönke Johnsen. “Freezing Behaviour Facilitates Bioelectric Crypsis in Cuttlefish Faced with Predation Risk.” *Proceedings of the Royal Society B: Biological Sciences* 282 (1820): 20151886. https://doi.org/10.1098/rspb.2015.1886.

Budelmann, Bernd U. 1998. “Autophagy in *Octopus*.” *South African Journal of Marine Sciences* 20 (1): 101–108. https://doi.org/10.2989/025776198784126502.

Burghardt, Gordon M. 2005. *The Genesis of Animal Play: Testing the Limits*. MIT Press.

Chung, Tzu-Ting, Anne-Sophie Darmaillacq, Ludovic Dickel, and Chuan-Chin Chiao. 2022. “The Effect of Unexpected Reward on Decision-Making in Cuttlefish.” *Scientific Reports* 12:2514. https://doi.org/10.1038/s41598-022-06443-w.

Cooke, Gavan M., Belinda M. Tonkins, and Jennifer A. Mather. 2019. “Care and Enrichment for Captive Cephalopods.” In *The Welfare of Invertebrate Animals*, edited by Claudio Carere and Jennifer A. Mather. Springer.

Dolan, R. J. 2002. “Emotion, Cognition, and Behavior.” *Science* 298 (5598): 1191–1194. https://doi.org/10.1126/science.1076358.

Drozd, Robert, Przemyslaw E. Cieslak, Michal Rychlik, Jan Rodriguez Parkitna, and Rafal Rygula. 2016. “Cognitive Judgment Bias Interacts with Risk Based Decision Making and Sensitivity to Dopaminergic Challenge in Male Rats.” *Frontiers in Behavioural Neuroscience* 10:163. https://doi.org/10.3389/fnbeh.2016.00163.

Fiorito, Graziano, Andrea Affuso, Jennifer A. Basil, et al. 2015. “Guidelines for the Care and Welfare of Cephalopods in Research—a Consensus Based on an Initiative by CephRes, FELASA and the Boyd Group.” *Laboratory Animals* 49 (S2): 1–90. https://doi.org/10.1177/0023677215580006.

Hanley, Janice S., Nadav Shashar, Roxanna Smolowitz, et al. 1998. “Modified Laboratory Culture Techniques for the European Cuttlefish *Sepia officinalis*.” *Biological Bulletin* 195 (2): 223–225. https://doi.org/10.2307/1542850.

Hayter, Leanne. 2005. *Husbandry Manual for Blue-Ringed Octopus*. TAFE NSW Ultimo. https://rares.world/wp-content/uploads/2019/07/Mollusca-Octopodidae-Hapalochlaena-lunulata-Blue-ringed-Octopus-2005LH-v-1.pdf.

Kuba, Michael J., Ruth A. Byrne, Daniela V. Meisel, and Jennifer A. Mather. 2006. “When Do Octopuses Play? Effects of Repeated Testing, Object Type, Age, and Food Deprivation on Object Play in *Octopus vulgaris*.” *Journal of Comparative Psychology* 120 (3): 184. https://doi.org/10.1037/0735-7036.120.3.184.

Kuba, Michael J., Daniela V. Meisel, Ruth A. Byrne, Ulrike Griebel, and Jennifer A. Mather. 2003. “Looking at Play in *Octopus vulgaris*.” In *Proceedings of the International Symposium Coleoid Cephalopods Through Time, 17-19 September, 2002, Berlin*, edited by Kerstin Warnke, Helmut Keupp, and Sigurd von Boletzly. Berliner Paläontologische Abhandlungen, vol 3. Freie Universität Berlin. https://www.researchgate.net/publication/286228905_Looking_at_play_in_Octopus_vulgaris.

Mather, Jennifer A., and Roland C. Anderson. 1999. “Exploration, Play and Habituation in Octopuses (*Octopus dofleini*).” *Journal of Comparative Psychology* 113 (3): 333–338. https://doi.org/10.1037/0735-7036.113.3.333.

McDonald, Kerrie. 2011. *Husbandry Guidelines for Mourning Cuttlefish*. TAFE NSW Richmond. https://aszk.org.au/wp-content/uploads/2020/03/Invertebrates.-Mourning-Cuttlefish-2012KM.pdf.

Nettle, Daniel, and Melissa Bateson. 2012. “The Evolutionary Origins of Mood and Its Disorders.” *Current Biology* 22 (17): R712–721. https://doi.org/10.1016/j.cub.2012.06.020.

Paul, Elizabeth S., Shlomi Sher, Marco Tamietto, Piotr Winkielman, and Michael T. Mendl. 2020. “Towards a Comparative Science of Emotion: Affect and Consciousness in Humans and Animals.” *Neuroscience and Biobehavioral Reviews* 108 (January): 749–770. https://doi.org/10.1016/j.neubiorev.2019.11.014.

Proctor, Helen S., Gemma Carder, and Amelia R. Cornish. 2013. “Searching for Animal Sentience: A Systematic Review of the Scientific Literature.” *Animals* 3 (3): 882–906. https://doi.org/10.3390/ani3030882.

Rowan, Andrew N., Joyce M. D’Silva, Ian J. H. Duncan, and Nicholas Palmer. 2021. “Animal Sentience: History, Science, and Politics.” *Animal Sentience* 31:1. https://doi.org/10.51291/2377-7478.1697.

Sherrill, Johanna, Lucy H. Spelman, Carrie L. Reidel, and Richard J. Montali. 2000. “Common Cuttlefish (*Sepia officinalis*) Mortality at the National Zoological Park: Implications for Clinical Management.” *Journal of Zoo and Wildlife Medicine* 31 (4): 523–531. https://doi.org/10.1638/1042-7260(2000)031[0523:CCSOMA]2.0.CO;2.

Zylinksi, Sarah. 2015. “Fun and Play in Invertebrates.” In “Biology of Fun.” Special issue, *Current Biology* 25 (1): R10–12. https://doi.org/10.1016/j.cub.2014.09.068.

CHAPTER 9

Pain

What is pain? The International Association for the Study of Pain defines pain as “an unpleasant sensory and emotional experience associated with, or resembling that associated with, actual or potential tissue damage”.[1] Sentience is much more than just the capacity to feel pain, but pain is an element with special significance for ethics and law.

Because pain is an *experience*, it goes beyond the mere detection of actual or potential tissue damage and beyond reflex responses. Think here of touching your hand against a hot stove. The hand withdraws, but this reflex response is controlled by the spinal cord and is already underway before you feel any pain.[2] The experience of pain occurs later, when information about the event reaches the parts of the brain involved in generating emotional experiences.[3] The experience is useful not because it triggers reflexes but because it allows you to tend and treat your injury, learn about the threat, and make better decisions in future.

Accordingly, to find evidence of pain in other animals, we need to look for responses to noxious stimulation (e.g. injury) that are more sophisticated than reflexes. Finding specialized neurons that detect noxious stimuli—*nociceptors*—is a relevant line of evidence but not enough by itself. We should also look for signs that information from the nociceptors is reaching integrative brain regions, as well as evidence that the information changes behavior, leading to rapid learning and avoidance behavior, wound-tending (or similar) behaviors over extended periods, and altered patterns of decision-making about opportunities and risks.

One experimental approach that can be used to probe questions of pain is a *conditioned place avoidance and preference test* (see Figure 18). An important study by Robyn Crook applied this approach to Bock's pygmy octopus (*Octopus bocki*).[4] The animals were presented with a free choice between two chambers. Their initial preferences were noted, then some received a noxious stimulus (an injection of acetic acid in their arm) and were placed in their preferred chamber to experience its effects. Later, some received a local anesthetic (lidocaine) on the injury and were placed in the other chamber to experience its effects. The question was: would these octopuses switch their preferences, developing a lasting aversion for the chamber where the effects of injury were experienced and a lasting preference for the chamber where the effects of the lidocaine were experienced? In mammals such as rats, this preference shift is taken as evidence of pain.[5] The octopuses displayed the same pattern (see Figure 19).

Moreover, Crook observed wound-tending-like behaviors: the injured octopuses would curl another arm around their injured arm and scrape at the skin as though trying to remove a toxic substance. Crook also recorded the activity in the nerves connecting the injured arm to the central brain (brachial connectives), showing a storm of activity that was silenced by the local anesthetic.

The evidence for pain in cuttlefish, though not as strong as for octopuses, is still strong. A recent study on juvenile pharaoh cuttlefish (*Sepia pharaonis*) showed wound-directed grooming (brushing their arms over the injected site) to areas that have been injected with acetic acid. This behavior stopped, just as in the case of octopuses, when lidocaine was applied.[6] There is no evidence yet of conditioned place preferences in cuttlefish, but this is because the experiments have not been done rather than because of any negative results.

Although the case is not as strong as for octopuses and cuttlefish, there is also substantial evidence of pain in squid. It is clear that squid have nociceptors and that injury produces long-term behavioral changes. In the longfin inshore squid (*Doryteuthis pealeii*), injury increases

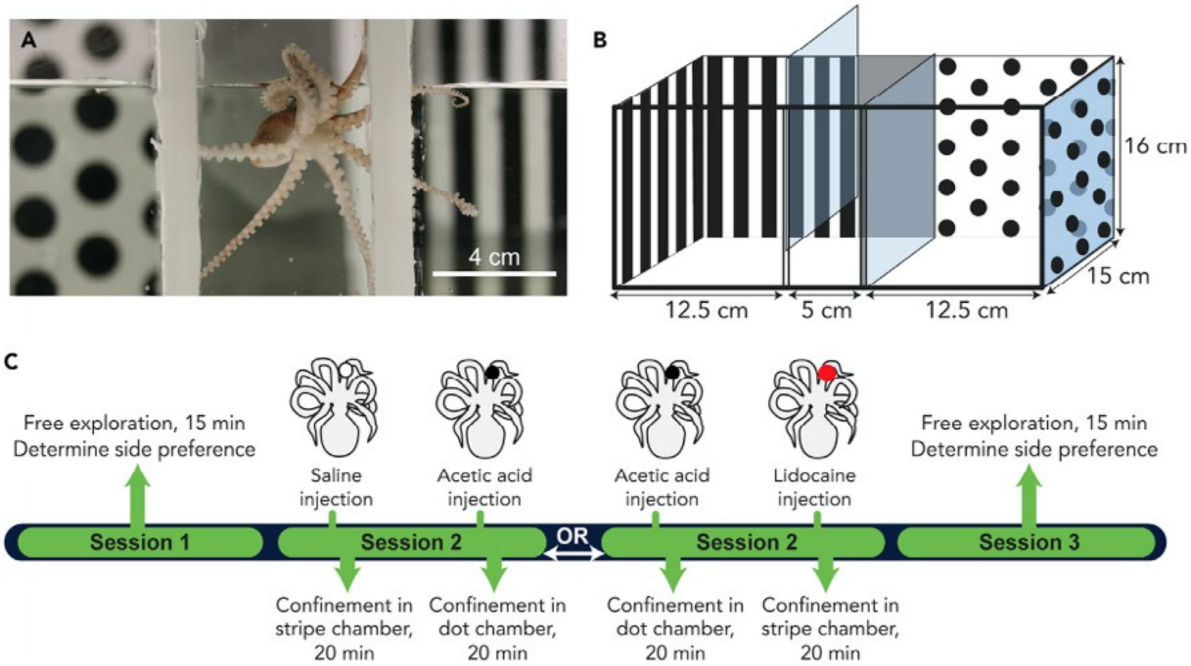

FIGURE 18. Crook's conditioned place avoidance and preference test for pain. *A*, Octopus in the apparatus. *B*, Diagram of the apparatus. *C*, Timeline of an experiment. In this example, an octopus showed a preference in session 1 for the dot chamber, so was given an injection of acetic acid prior to confinement in the dot chamber and/or lidocaine prior to confinement in the striped chamber, to see whether its preferences would reverse. Reproduced from Crook, "Behavioural and Neurophysiological Evidence Suggests Affective Pain Experience in Octopus." / CC-BY-NC-ND 4.0.

responsiveness to subsequent threats[7] and increases the propensity to school (i.e. seek protection in a group).[8] In the Hawaiian bobtail squid (*Euprymna scolopes*), injury early in life has long-term consequences for decision-making later, making the animals permanently more cautious around predators.[9]

A comprehensive review of the evidence in 2021 (involving two of the authors of this summary, Birch and Schnell) concluded that there is very strong evidence of pain in octopuses and substantial evidence in squid and cuttlefish.[10] There is very little evidence one way or the other concerning nautiluses. To err on the side of caution, however, we should assume that all cephalopods—not just octopuses—are capable of experiencing pain.

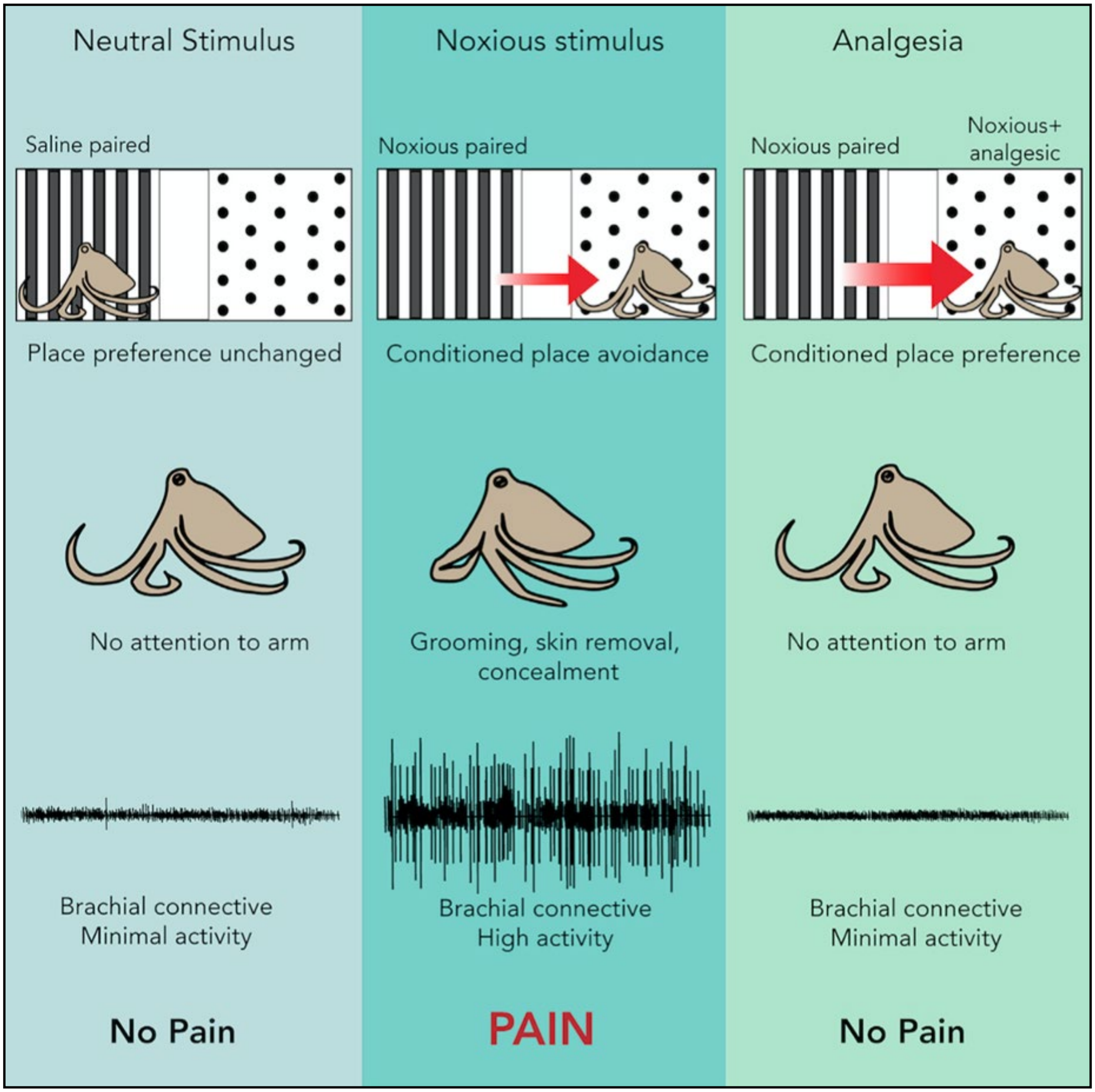

FIGURE 19. A graphical representation of the results of Crook's conditioned place avoidance and preference test. Reproduced from Crook, "Behavioural and Neurophysiological Evidence Suggests Affective Pain Experience in Octopus." / CC-BY-NC-ND 4.0.

References

1 Raja et al. 2020

2 Derderian et al. 2023

3 De Ridder et al. 2021

4 Crook 2021

5 Navratilova et al. 2013

6 Kuo et al. 2022

7 Crook et al., 2014

8 Oshima et al. 2016

9 Howard et al. 2019

10 Birch et al. 2021

Key Texts

Birch, Jonathan, Charlotte Burn, Alexandra K. Schnell, Heather Browning, and Andrew Crump. 2021. *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans*, commissioned by the Department for Environment, Food, & Rural Affairs (Defra). London School of Economics and Political Science. https://www.lse.ac.uk/business/consulting/assets/documents/Sentience-in-Cephalopod-Molluscs-and-Decapod-Crustaceans-Final-Report-November-2021.pdf.

This comprehensive review found very strong evidence of pain in octopuses and substantial evidence in squid and cuttlefish, leading to the inclusion of cephalopods (along with decapod crustaceans such as true crabs and lobsters) in the UK's Animal Welfare (Sentience) Act 2022.

Crook, Robyn J. 2021. "Behavioural and Neurophysiological Evidence Suggests Affective Pain Experience in Octopus." *iScience* 24 (3): 102229. https://doi.org/10.1016/j.isci.2021.102229.

This demonstration of "conditioned place preference" in octopuses provides especially compelling evidence of pain.

Fiorito, Graziano, Andrea Affuso, Jennifer A. Basil, et al. 2015. "Guidelines for the Care and Welfare of Cephalopods in Research—a Consensus Based on an Initiative by CephRes, FELASA and the Boyd Group." *Laboratory Animals* 49 (S2): 1–90. https://doi.org/10.1177/0023677215580006.

This initiative led to guidelines for the care of cephalopod molluscs in research. In the European Union, United Kingdom, Canada, Switzerland, Norway, and parts of Australia, animal welfare law requires humane treatment of cephalopods used in scientific research.

Kuo, Tzu-Hsin, Lynne U. Sneddon, Joseph W. Spencer, and Chuan-Chin Chiao. 2022. "Impact of Lidocaine on Pain-Related Grooming in Cuttlefish." *Biology* 11 (11): 1560. https://doi.org/10.3390/biology11111560.

This study shows wound-tending behavior in cuttlefish (grooming directed at the site of an injury) and shows it to be reduced by a local anesthetic, lidocaine, a pattern we would expect if the injury causes an experience of pain that the lidocaine relieves.

Bibliography

Alupay, Jean S., Stavros P. Hadjisolomou, and Robyn J. Crook. 2014. “Arm Injury Produces Long-Term Behavioral and Neural Hypersensitivity in Octopus.” *Neuroscience Letters 558:*137–142. https://doi.org/10.1016/j.neulet.2013.11.002.

Andrews, Paul L. R., Anne-Sophie Darmaillacq, Ngaire Dennison, et al. 2013. “The Identification and Management of Pain, Suffering and Distress in Cephalopods, Including Anaesthesia, Analgesia and Humane Killing.” In “Cephalopod Biology,” edited by Graziano Fiorito and Giovanna Ponte. Special issue, *Journal of Experimental Marine Biology and Ecology* 447 (September): 46–64. https://doi.org/10.1016/j.jembe.2013.02.010.

Barlow, J. J., and G. D. Sanders. 1974. “Intertrial Interval and Passive Avoidance Learning in *Octopus vulgaris*.” *Animal Learning & Behavior* 2 (2): 86–88. https://doi.org/10.3758/BF03199127.

Bazarini, Stephanie N., and Robyn J. Crook. 2020. “Environmental Estrogen Exposure Disrupts Sensory Processing and Nociceptive Plasticity in the Cephalopod *Euprymna scolopes*.” *Journal of Experimental Biology* 223 (12): jeb218008. https://doi.org/10.1242/jeb.218008.

Bedore, Christine N., Stephen M. Kajiura, and Sönke Johnsen. “Freezing Behaviour Facilitates Bioelectric Crypsis in Cuttlefish Faced with predation risk.” *Proceedings of the Royal Society B: Biological Sciences* 282 (1820): 20151886. https://doi.org/10.1098/rspb.2015.1886.

Birch, Jonathan, Charlotte Burn, Alexandra K. Schnell, Heather Browning, and Andrew Crump. 2021. *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans*, commissioned by the Department for Environment, Food, & Rural Affairs (Defra). London School of Economics and Political Science. https://www.lse.ac.uk/business/consulting/assets/documents/Sentience-in-Cephalopod-Molluscs-and-Decapod-Crustaceans-Final-Report-November-2021.pdf.

Broom, Donald M. 2014. *Sentience and Animal Welfare*. CABI.

Butler-Struben, Hanna M., Samantha M. Brophy, Nasira A. Johnson, and Robyn J. Crook. 2018. “In Vivo Recording of Neural and Behavioral Correlates of Anesthesia Induction, Reversal, and Euthanasia in Cephalopod Molluscs.” *Frontiers in Physiology* 9:109. https://doi.org/10.3389/fphys.2018.00109.

Crook, Robyn J. 2021. “Behavioural and Neurophysiological Evidence Suggests Affective Pain Experience in Octopus.” *iScience* 24 (3): 102229. https://doi.org/10.1016/j.isci.2021.102229.

Crook, Robyn J., Katharine Dickson, Roger T. Hanlon, and Edgar T. Walters. 2014. “Nociceptive Sensitization Reduces Predation Risk.” *Current Biology* 24 (10): 1121–1125. https://doi.org/10.1016/j.cub.2014.03.043.

Crook, Robyn J., Roger T. Hanlon, and Edgar T. Walters. 2013. “Squid Have Nociceptors That Display Widespread Long-Term Sensitization and Spontaneous Activity after Bodily Injury.” *Journal of Neuroscience* 33 (24): 10021–10026. https://doi.org/10.1523/JNEUROSCI.0646-13.2013.

Crook, Robyn J., Trevor Lewis, Roger T. Hanlon, and Edgar T. Walters. 2011. “Peripheral Injury Induces Long-Term Sensitization of Defensive Responses to Visual and Tactile Stimuli in the Squid *Loligo pealeii*, Lesueur 1821.” *Journal of Experimental Biology* 24 (19): 3171–3185. https://doi.org/10.1242/jeb.058131.

Crook, Robyn J., and Edgar T. Walters. 2011. “Nociceptive Behavior and Physiology of Molluscs: Animal Welfare Implications.” *ILAR Journal* 52 (2): 185–195. https://doi.org/10.1093/ilar.52.2.185.

della Rocca, Giorgia, Alessandra Di Salvo, Giacomo Giannettoni, and Mary Ellen Goldberg. 2015. “Pain and Suffering in Invertebrates: An Insight on Cephalopods.” *American Journal of Animal and Veterinary Sciences* 10 (2): 77–84. https://doi.org/10.3844/ajavsp.2015.77.84.

De Ridder, Dirk, Divya Adhi, and Sven Vanneste. 2021. “The Anatomy of Pain and Suffering in the Brain and Its Clinical Implications.” *Neuroscience & Biobehavioral Reviews* 130 (November): 125–146. https://doi.org/10.1016/j.neubiorev.2021.08.013.

Derderian, Celena, Karlie R. Shumway, and Prasanna Tadi. 2023. “Physiology, Withdrawal Response.” In *StatPearls*. StatPearls Publishing. https://www.ncbi.nlm.nih.gov/books/NBK544292/.

Deutsch, Skyler, Rachel Parsons, Jonathan Shia, et al. 2023. “Evaluation of Candidates for Systemic Analgesia and General Anesthesia in the Emerging Model Cephalopod, *Euprymna berryi*.” *Biology* 12 (2): 201. https://doi.org/10.3390/biology12020201.

Di Cristina, Giulia. 2017. “Nociception in the Cephalopod Mollusc *Octopus vulgaris*: A Contribution to Mapping Putative Nociceptors in the Octopus Arm.” PhD diss., Università degli Studi di Napoli Federico II. https://core.ac.uk/reader/153401140.

Fiorito, Graziano, Andrea Affuso, Jennifer A. Basil, et al. 2015. “Guidelines for the Care and Welfare of Cephalopods in Research—a Consensus Based on an Initiative by CephRes, FELASA and the Boyd Group.” *Laboratory Animals* 49 (S2): 1–90. https://doi.org/10.1177/0023677215580006.

Frazier, D. T., M. Ohta, and T. Narahashi. 1973. “Nature of the Morphine Receptor Present in the Squid Axon.” *Experimental Biology and Medicine* 142 (4): 1209–1214. https://doi.org/10.3181/00379727-142-37210.

Hague, Theresa, Michaela Florini, and Paul L. R. Andrews. 2013. “Preliminary In Vitro Functional Evidence for Reflex Responses to Noxious Stimuli in the Arms of *Octopus vulgaris*.” In “Cephalopod Biology,” edited by Graziano Fiorito and Giovanna Ponte. Special issue, *Journal of Experimental Marine Biology and Ecology* 447 (September): 100–105. https://doi.org/10.1016/j.jembe.2013.02.016.

Howard, Ryan B., Lauren N. Lopes, Christina R. Lardie, Paul P. Perez, and Robyn J. Crook. 2019. "Early-Life Injury Produces Lifelong Neural Hyperexcitability, Cognitive Deficit and Altered Defensive Behaviour in the Squid *Euprymna scolopes*." In "Evolution of Mechanisms and Behaviour Important for Pain," edited by Edgar T. Walters and Amanda C. de C. Williams. Theo Murphy meeting issue, *Philosophical Transactions of the Royal Society B: Biological Sciences* 374 (1785): 20190281. https://doi.org/10.1098/rstb.2019.0281.

Kuo, Tzu-Hsin, Lynne U. Sneddon, Joseph W. Spencer, and Chuan-Chin Chiao. 2022. "Impact of Lidocaine on Pain-Related Grooming in Cuttlefish." *Biology* 11 (11): 1560. https://doi.org/10.3390/biology11111560.

Mason, Georgia J. 2011. "Invertebrate Welfare: Where is the Real Evidence for Conscious Affective States?" *Trends in Ecology and Evolution* 26 (5): 212–213. https://doi.org/10.1016/j.tree.2011.02.009.

Mellor, David J. 2012. "Animal Emotions, Behaviour and the Promotion of Positive Welfare States." *New Zealand Veterinary Journal* 60 (1): 1–8. https://doi.org/10.1080/00480169.2011.619047.

Mellor, David J. 2019. "Welfare-Aligned Sentience: Enhanced Capacities to Experience, Interact, Anticipate, Choose and Survive." In "Domestic Animal Behavior and Well-Being," edited by Matthew Jorgensen and Jesse Andrew Robbins. Special issue, *Animals* 9 (7): 440. https://doi.org/10.3390/ani9070440.

Navratilova, Edita, Jennifer Yanhua Xie, Tamara King, and Frank Porreca. 2013. "Evaluation of Reward from Pain Relief." *Annals of the New York Academy of Sciences* 1282 (1): 1–11. https://doi.org/10.1111/nyas.12095.

Negus, S. Stevens, Edward J. Bilsky, Gail Pereira Do Carmo, and Glenn W. Stevenson. 2010. "Rationale and Methods for Assessment of Pain-Depressed Behavior in Preclinical Assays of Pain and Analgesia." In *Analgesia: Methods and Protocols*, edited by Arpad Szallasi. Methods in Molecular Biology 617. Humana Press.

Oshima, Megum, Theodor di Pauli von Treuheim, Julia Carroll, Roger T. Hanlon, Edgar T. Walters, and Robyn J. Crook. 2016. "Peripheral Injury Alters Schooling Behavior in Squid, *Doryteuthis pealeii*." *Behavioral Processes* 128 (July): 89–95. https://doi.org/10.1016/j.beproc.2016.04.008.

Perez, Paul V., Hanna M. Butler-Struben, and Robyn J. Crook. 2017. "The Selective Serotonin Reuptake Inhibitor Fluoxetine Increases Spontaneous Afferent Firing, but Not Mechanonociceptive Sensitization, in Octopus." *Invertebrate Neuroscience* 17 (4): 10. https://doi.org/10.1007/s10158-017-0203-1.

Raja, Srinivasa N., Daniel B. Carr, Milton Cohen, et al. 2020. "The Revised International Association for the Study of Pain Definition of Pain: Concepts, Challenges, and Compromises." *Pain* 161 (9): 1976–1982. https://doi.org/10.1097/j.pain.0000000000001939

Ross, D. M. 1971. "Protection of Hermit Crabs (*Dardanus* spp.) from Octopus by Commensal Sea Anemones (*Calliactis* spp.)." *Nature* 230 (5283): 401–402. https://doi.org/10.1038/230401a0.

Sadler, Katelyn E., Jeffrey S. Mogil, and Cheryl L. Stucky. 2022. “Innovations and Advances in Modelling and Measuring Pain in Animals.” *Nature Reviews Neuroscience* 23 (2): 70–85. https://doi.org/10.1038/s41583-021-00536-7.

Shomrat, Tal, N. Feinstein, M. Klein, and Binyamin Hochner. 2010. “Serotonin is a facilitatory neuromodulator of synaptic transmission and “reinforces” long-term potentiation induction in the vertical lobe of *Octopus vulgaris*.” *Neuroscience* 169 (1): 52–64. https://doi.org/10.1016/j.neuroscience.2010.04.050.

Smith, Jane A., and Kenneth M. Boyd, eds. 1991. *Lives in the Balance: The Ethics of Using Animals in Biomedical Research*. Oxford University Press.

Smith, Ewan St. John, and Gary R. Lewin. 2009. “Nociceptors: A Phylogenetic View.” *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 195 (12): 1089–1106. https://doi.org/10.1007/s00359-009-0482-z.

Sneddon, Lynne U., Robert W. Elwood, Shelley A. Adamo, and Matthew C. Leach. 2014. “Defining and Assessing Animal Pain.” *Animal Behaviour* 97 (November): 201–212. https://doi.org/10.1016/j.anbehav.2014.09.007.

Stefano, George B., Beverly Hall, Maynard H. Makman, and Bernyce Dvorkin. 1981. “Opioid Inhibition of Dopamine Release from Nervous Tissue of *Mytilus edulis* and *Octopus bimaculatus*.” *Science* 213 (4510): 928–930. https://doi.org/10.1126/science.6266017.

Walters, Edgar T. 2018. “Nociceptive Biology of Molluscs and Arthropods: Evolutionary Clues About Functions and Mechanisms Potentially Related to Pain.” *Frontiers in Physiology* 9:1049. https://doi.org/10.3389/fphys.2018.01049.

CHAPTER 10

Key Welfare Needs

Caring for the physical and mental wellbeing of animals of other species always requires a deep understanding of that species' physiology, ecology, behavior, and cognition. Currently, cephalopods are kept in human-controlled environments for various purposes.[1] They are commonly displayed in public aquariums around the world. For more than 100 years, they have also been used as experimental animals in scientific research.[2],[3],[4] Moreover, apparently increasing demand for cephalopods for human consumption[5],[6] has been driving controversial attempts to farm octopuses commercially on a large scale.[7]

Although welfare guidance for cephalopods has existed since at least 1928,[8] it is fair to say this group has been relatively neglected in the field of animal welfare science.[9] However, accumulating evidence in support of their sentience, capacity for pain (see "Pain"), and cognitive sophistication (see "Problem Solving and Intelligence," "Learning and Memory").have been leading to governmental and scientific initiatives to build better laws, regulations, and guidelines. One recent example was the recognition of cephalopods (along with decapod crustaceans) as sentient beings by the UK government's Animal Welfare (Sentience) Act 2022. Another was the inclusion of cephalopods in the European Union Directive 2010/63/EU, which regulates the use of animals for scientific research.[10],[11] Following this legal milestone, an international team of researchers developed guidelines for the care and welfare of cephalopods in research.[12] This work provided valuable yet broad recommendations about the best conditions and practices related to the capture, transport, welfare monitoring, anesthesia, euthanasia, and husbandry of cephalopods.

Known welfare needs

As for all aquatic animals, water features—including temperature, salinity, and quality (e.g., O_2, CO_2, pH, nitrogenous compounds)—are vital for the wellbeing of cephalopods. These parameters must be monitored constantly and adjusted according to the specific physiological needs of each species.

Particular attention should be paid to the monitoring of dissolved oxygen and nitrogenous compounds. This is because cephalopods have, respectively, fast metabolic rates[13],[14] and carnivorous diets.[15] Protein-rich food may lead to the accumulation of nitrogenous compounds in toxic concentrations, leading to adverse effects on the organism's physiology and behavior.[16]

The features of the enclosure also play a fundamental role in the welfare of cephalopods and must be designed carefully on the basis of several factors, such as the lifestyle and body size of the animal. Because most octopuses and cuttlefish are benthic species (that is, they spend most of their time in contact or in proximity to the seafloor), the size of the bottom surface of the tank is particularly relevant.[12] The presence of dens, sheltered areas, or sandy substrates (for sand-dwelling species) is a crucial requirement for these species.[12],[17] The lack of such elements may induce high levels of stress.[18]

Meanwhile, the depth and shape of the enclosure are especially relevant for cephalopods that spend most of their time far from the seafloor. For example, cylindrical tanks are recommended for nautiluses to accommodate their natural vertical migration in the water column;[19] circular or elliptical tanks are considered more appropriate for pelagic squids to better support their natural locomotion while also limiting chances of physical injury from hitting solid corners.[20],[16]

The complexity of the physical and social environment also needs consideration. Several species live in complex physical habitats, such as coral reefs and seagrass meadows. In these cases, physical enrichment (e.g., inclusion of natural elements like stones and corals in the tanks) is recommended as it can encourage the expression of natural behaviors, such as object manipulation and food-searching activities in octopuses.[21],[22],[23]

Social systems and natural social tendencies vary a great deal between species (see "Sociality and Mating Strategies"). For gregarious species like most squids, group housing is encouraged.[20] When housing a group together in the same tank, it is crucial to adjust stocking densities, sex ratio, and body size differences to fit both species-specific needs and the features of the enclosure.

By contrast, most octopuses typically display weak social tolerance and even cannibalistic tendencies.[24] Individual housings are therefore recommended for these species.[12] The presence of other octopuses in confined spaces may induce distress and aggressive interactions, whose escalation could lead to physical injuries and potentially fatalities, particularly in cases of large differences in body size among the animals. We also note, however, that octopuses have occasionally been observed living in high densities and clumped dens in the wild (e.g., *Octopus tetricus*[25] and *Octopus vulgaris*[26]). This suggests that the ability of some octopus species to tolerate other octopuses may be greater than traditionally assumed.

Another key consideration is that the welfare needs of cephalopods vary hugely. There are more than 800 cephalopod species, which differ dramatically in their biological adaptations, lifestyles, ecology (e.g., diet, habitats), social systems, and behavior (see "Diversity of the Cephalopods").[27] Importantly, welfare needs can vary substantially between closely-related species and even within the lifespan of an individual.[12],[28] The hatchlings (paralarvae) of species like *Octopus vulgaris* resemble small squid-like creatures that live in the water column, rather than miniatures of the adults living on the seafloor.[29] A few weeks after hatching, the paralarvae settle down, acquire the typical appearance of an octopus, and subsequently undertake very rapid growth. This marked variation in lifestyle as well as in size (from a few grams, up to 10 kg in *O. vulgaris*) is matched by an equivalent variation in welfare needs.

One of the major challenges in the field of cephalopod welfare is refining current guidelines and practices in order to address this enormous variability, both within and between species, in welfare needs. Recently, important steps have been taken in this direction through the production of more detailed recommendations for the care of some of the species most commonly used in research.[30] However, many gaps remain to be filled. In addition, substantial efforts should also be dedicated to developing more effective procedures for assessing cephalopod health and welfare (see “Knowledge Gaps”).

References

1 Nakajima et al. 2018

2 O'Brien et al. 2018

3 Di Cosmo et al. 2021

4 Rosa et al. 2024

5 FAO 2020

6 Ospina-Alvarez et al. 2022

7 Jacquet et al. 2024

8 Grimpe 1928

9 De Sio et al. 2020

10 Smith et al 2013

11 Di Cristina et al. 2015

12 a b c d e Fiorito et al. 2015

13 Seibel 2007

14 Ikeda 2016

15 Villanueva et al. 2017

16 a b Bolezky and Hanlon 1983

17 Panetta et al. 2017

18 Hu et al. 2024

19 Crook et al. 2009

20 a b Hanlon 1990

21 Anderson and Wood 2001

22 Yasumuro and Ikeda 2011

23 Cooke et al. 2019

24 Ibanez and Keyl 2010

25 Scheel et al. 2016

26 Guerra et al. 2014

27 Hanlon and Messenger 2018

28 Robin et al. 2014

29 Vidal and Shea 2023

30 Ponte et al. 2023

Key Texts

Fiorito, Graziano, Andrea Affuso, Jennifer A. Basil, et al. 2015. "Guidelines for the Care and Welfare of Cephalopods in Research—a Consensus Based on an Initiative by CephRes, FELASA and the Boyd Group." *Laboratory Animals* 49 (S2): 1–90. https://doi.org/10.1177/0023677215580006.

This study provides key guidelines and recommendations for the use of cephalopods in research, including recommendations for the capture, transport, husbandry, welfare monitoring, anesthesia, and euthanasia.

Ponte, Giovanna, Katina Roumbedakis, COST Action FA1301, et al. 2023. "General and Species-Specific Recommendations for Minimal Requirements for the Use of Cephalopods in Scientific Research." *Laboratory Animals* 57 (1): 26–39. https://doi.org/10.1177/00236772221111261.

This study provides species-specific recommendations for the care and welfare of the most used cephalopods in research.

Bibliography

Anderson, Roland C., and James B. Wood. 2001. “Enrichment for Giant Pacific Octopuses: Happy as a Clam?” *Journal of Applied Animal Welfare Science* 4 (2): 157–168. https://doi.org/10.1207/S15327604JAWS0402_10.

Birch, Jonathan, Charlotte Burn, Alexandra K. Schnell, Heather Browning, and Andrew Crump. 2021. *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans*, commissioned by the Department for Environment, Food, & Rural Affairs (Defra). London School of Economics and Political Science. https://www.lse.ac.uk/business/consulting/assets/documents/Sentience-in-Cephalopod-Molluscs-and-Decapod-Crustaceans-Final-Report-November-2021.pdf.

Boletzky, Sigurd von, and Roger T. Hanlon. 1983. “A Review of the Laboratory Maintenance, Rearing and Culture of Cephalopod Molluscs.” *Memoirs of the National Museum of Victoria* 44:147–187. https://doi.org/10.24199/j.mmv.1983.44.11.

Cooke, Gavan M., Belinda M. Tonkins, and Jennifer A. Mather. 2019. “Care and Enrichment for Captive Cephalopods.” In *The Welfare of Invertebrate Animals*, edited by Claudio Carere and Jennifer A. Mather. Springer.

Crook, Robyn J., Roger T. Hanlon, and Jennifer A. Basil. 2009. “Memory of Visual and Topographical Features Suggests Spatial Learning in Nautilus (*Nautilus pompilius* L.).” *Journal of Comparative Psychology* 123 (3): 264–274. https://doi.org/10.1037/a0015921.

De Sio, Fabio, Frederike D. Hanke, Kerstin Warnke, et al. 2020. “E Pluribus Octo—Building Consensus on Standards of Care and Experimentation in Cephalopod Research: A Historical Outlook.” *Frontiers in Physiology* 11:645. https://doi.org/10.3389/fphys.2020.00645.

Di Cristina, Giulia, Paul L. R. Andrews, Giovanna Ponte, Viola Galligioni, and Graziano Fiorito. 2015. “The Impact of Directive 2010/63/EU on Cephalopod Research.” *Invertebrate Neuroscience* 15 (4): 8. https://doi.org/10.1007/s10158-015-0183-y.

FAO (Food and Agriculture Organization of the United Nations). 2020. *The State of World Fisheries and Aquaculture 2020*. FAO. https://doi.org/10.4060/ca9229en.

Fiorito, Graziano, Andrea Affuso, Jennifer A. Basil, et al. 2015. “Guidelines for the Care and Welfare of Cephalopods in Research—a Consensus Based on an Initiative by CephRes, FELASA and the Boyd Group.” *Laboratory Animals* 49 (S2): 1–90. https://doi.org/10.1177/0023677215580006.

Grimpe, Georg. 1928. “Pflege, Behandlung und Zucht der Cephalopoden für zoologische und physiologische Zwecke.” In *Handbuch der Biologischen Arbeitsmethoden*, edited by Emil Äberhalden. Verlag Urban & Schwarzenberg.

Guerra, Ángel, Jorge Hernández-Urcera, Manuel E. Garci, et al. 2014. “Dwellers in Dens on Sandy Bottoms: Ecological and Behavioural Traits of *Octopus vulgaris*.” *Scientia Marina* 78 (3): 405–414. https://doi.org/10.3989/scimar.04071.28F.

Hanlon Roger T. 1990. “Maintenance, Rearing, and Culture of Teuthoid and Sepioid Squids.” In *Squid as Experimental Animals*, edited by Daniel L. Gilbert, William J. Adelman, and John M. Arnold. Springer.

Hanlon, Roger T., and John B. Messenger. 2018. *Cephalopod Behaviour*. 2nd ed. Cambridge University Press.

Hu, Yuanhai, Jian Zheng, Fei Han, et al. 2024. “Effects of Shelter on the Welfare of Juvenile *Amphioctopus fangsiao*: Survival, Growth, Behavior and Physiology.” *Aquaculture* 578:740040. https://doi.org/10.1016/j.aquaculture.2023.740040.

Ibáñez, Christian M., and Friedemann Keyl. 2010. “Cannibalism in Cephalopods.” *Reviews in Fish Biology and Fisheries* 20 (1): 123–136. https://doi.org/10.1007/s11160-009-9129-y.

Ikeda, Tsutomu. 2016. “Routine Metabolic Rates of Pelagic Marine Fishes and Cephalopods as a Function of Body Mass, Habitat Temperature and Habitat Depth.” *Journal of Experimental Marine Biology and Ecology* 480 (July): 74–86. https://doi.org/10.1016/j.jembe.2016.03.012.

Jacquet, Jennifer, Becca Franks, Peter Godfrey-Smith, et al. 2024. “Support US OCTOPUS Act to Keep Octopuses Wild.” *Science* 385 (6710): 721–722. https://doi.org/10.1126/science.adr3813.

Nakajima, Ryuta, Shuichi Shigeno, Letizia Zullo, Fabio De Sio, and Markus R. Schmidt. 2018. “Cephalopods Between Science, Art, and Engineering: A Contemporary Synthesis.” *Frontiers in Communication* 3:20. https://doi.org/10.3389/fcomm.2018.00020.

O’Brien, Caitlin E., Katina Roumbedakis, and Inger E. Winkelmann. 2018. “The Current State of Cephalopod Science and Perspectives on the Most Critical Challenges Ahead From Three Early-Career Researchers.” *Frontiers in Physiology* 9:700. https://doi.org/10.3389/fphys.2018.00700.

Ospina-Alvarez, Andres, Silvia de Juan, Pablo Pita, et al. 2022. “A Network Analysis of Global Cephalopod Trade.” *Scientific Reports* 12:322. https://doi.org/10.1038/s41598-021-03777-9.

Panetta, Deanna, M. Solomon, Kendra C. Buresch, and Roger T. Hanlon. 2017. “Small-Scale Rearing of Cuttlefish (*Sepia officinalis*) for Research Purposes.” *Marine and Freshwater Behaviour and Physiology* 50 (2): 115–124. https://doi.org/10.1080/10236244.2017.1343631.

Ponte, Giovanna, Katina Roumbedakis, COST Action FA1301, et al. 2023. “General and Species-Specific Recommendations for Minimal Requirements for the Use of Cephalopods in Scientific Research.” *Laboratory Animals* 57 (1): 26–39. https://doi.org/10.1177/00236772221111261.

Robin, Jean-Paul, Michael Roberts, Lou Zeidberg, et al. 2014. “Transitions During Cephalopod Life History: The Role of Habitat, Environment, Functional Morphology and Behaviour.” In *Advances in Cephalopod Science: Biology, Ecology, Cultivation and Fisheries*, edited by Erica A. G. Vidal. Advances in Marine Biology 67. Academic Press.

Rosa, Rui Rosa, Catarina P. Santos, Francisco Borges, et al. 2024. “Past, Present, and Future Trends in Octopus Research.” In *Octopus Biology and Ecology*, edited by Rui Rosa, Ian Gleadall, Graham Pierce, and Roger Villanueva. Academic Press.

Seibel, Brad A. 2007. “On the Depth and Scale of Metabolic Rate Variation: Scaling of Oxygen Consumption Rates and Enzymatic Activity in the Class Cephalopoda (Mollusca).” *Journal of Experimental Biology* 210 (1): 1–11. https://doi.org/10.1242/jeb.02588.

Scheel, David, Peter Godfrey-Smith, and Matthew Lawrence. 2016. “Signal Use by Octopuses in Agonistic Interactions.” *Current Biology* 26 (3): 377–382. https://doi.org/10.1016/j.cub.2015.12.033.

Schnell, Alexandra K., Piero Amodio, Markus Boeckle, and Nicola S. Clayton. 2021. “How Intelligent is a Cephalopod? Lessons from Comparative Cognition.” *Biological Reviews* 96 (1): 162–178. https://doi.org/10.1111/brv.12651.

Smith, Jane A., Paul L. R. Andrews, Penny Hawkins, Susanna Louhimies, Giovanna Ponte, and Ludovic Dickel. 2013. “Cephalopod Research and EU Directive 2010/63/EU: Requirements, Impacts and Ethical review.” In “Cephalopod Biology,” edited by Graziano Fiorito and Giovanna Ponte. Special issue, *Journal of Experimental Marine Biology and Ecology* 447 (September): 31–45. https://doi.org/10.1016/j.jembe.2013.02.009.

Vidal, Erica A. G., and Elizabeth K. Shea. 2023. “Cephalopod Ontogeny and Life Cycle Patterns.” *Frontiers in Marine Science* 10:1162735. https://doi.org/10.3389/fmars.2023.1162735.

Villanueva, Roger, Valentina Perricone, and Graziano Fiorito. 2017. “Cephalopods as Predators: A Short Journey Among Behavioral Flexibilities, Adaptions, and Feeding Habits.” *Frontiers in Physiology* 8:598. https://doi.org/10.3389/fphys.2017.00598.

Webster, John. 2005. *Animal Welfare: Limping Towards Eden; A Practical Approach to Redressing the Problem of Our Dominion Over the Animals*. UFAW Animal Welfare Series. Wiley-Blackwell.

Yasumuro, Haruhiko, and Yuzuru Ikeda. 2011. “Effects of Environmental Enrichment on the Behavior of the Tropical Octopus *Callistoctopus aspilosomatis*.” *Marine and Freshwater Behaviour and Physiology* 44 (3): 143–157. https://doi.org/10.1080/10236244.2011.598643.

CHAPTER 11

Knowledge Gaps

There is much we still do not know about the cephalopods—and many areas where new evidence would be incredibly valuable.

Cognition in Cephalopods

Cephalopods exhibit various sophisticated cognitive abilities (see "Problem Solving and Intelligence," "Learning and Memory"), which makes them intriguing subjects for scientific study. Despite extensive reviews on cephalopod behavior, body patterning, and learning abilities,[1],[2],[3],[4],[5] gaps in our understanding of their cognition remain.

WHY DID CEPHALOPOD INTELLIGENCE EVOLVE?

A big-picture knowledge gap concerns the evolution of complex cognition in cephalopods. According to the "social intelligence" hypothesis, complex social interactions drive the evolution of cognition. However, cephalopods demonstrate advanced cognitive abilities even though they do not live in complex social environments. This indicates that other evolutionary pressures may be at play when selecting for intelligent traits.[6],[5] By comparing cephalopods with other groups of animals, we can study how different selective pressures may have shaped the evolution of intelligence.

HOW DO BRAIN AND BEHAVIOR RELATE?

Cephalopods are renowned for their extraordinary behavioral flexibility, supported by sophisticated brain mechanisms. Despite this, the precise relationship between their brain organization and their behavioral flexibility remains inadequately understood. Current research highlights the complexity of cephalopod neural systems but often falls short of connecting specific neural structures to particular behaviors. Further investigation is needed to map these mechanisms to their corresponding behavioral functions.[7],[8]

Recent advances in cephalopod neuroscience have shed light on the cellular, molecular, and synaptic mechanisms underpinning their nervous systems.[9],[10] However, there is still a need for comprehensive studies on how these neurological mechanisms relate to higher cognitive functions. Future research is likely to shed new light on the molecular pathways and synaptic connections involved in complex behaviors and cognition and how these compare to mechanisms in other species.[11],[12]

LEARNING AND MEMORY

Research on cephalopod learning and memory has provided valuable insights into their cognitive abilities, with studies exploring many kinds of learning.[3],[13],[6],[5] However, there remains a gap in understanding the full spectrum of learning types and the underlying brain mechanisms involved.

For instance, some cephalopod species have demonstrated the ability to remember past events[14],[15] and plan for imminent future scenarios by delaying gratification,[16] showcasing advanced abilities for thinking about time. It remains unclear how many cephalopod species have these abilities. Moreover, it remains unclear whether they can plan for the *distant* future. Moreover, detailed studies are required to delineate how cephalopods encode, store, and retrieve memories.[17],[5],[18]

HOW ARE THE MINDS OF CEPHALOPODS SHAPED BY THEIR SENSORY ABILITIES?

Cephalopods possess highly developed sensory systems, particularly in vision and equilibrium (that is, monitoring changes in their body's position and motion).[19],[20] Yet the relation between sensory and cognitive processes is not yet well understood. Future research is likely to provide more insight into how cephalopods process sensory inputs to inform decision-making.[21],[22]

The Welfare of Cephalopods

The welfare of cephalopods has increasingly come under scrutiny. Although enough is already known to inform welfare regulations (see "Key Welfare Needs"), major evidence gaps remain.

ANESTHESIA AND PAIN RELIEF

The development of reliable anesthetic procedures for cephalopods is still in progress. Various substances have been tested with mixed success[23],[24] and there is still much to learn about their mechanisms and effects.[25],[26],[27] Magnesium chloride and ethyl alcohol have shown the most promising results, particularly in both tropical octopus and cuttlefish species[28] as well as temperate species.[29] The effectiveness of these anesthetics depends on various factors including age, sex, life stage, and environmental conditions, all of which remain insufficiently explored. It would be useful to develop pain scales similar to those used for mammals[30] and to explore ways for cephalopods to self-administer pain relief when they need it.[31],[32]

In the development of anesthetics, there is a need to distinguish reliably between immobilization and genuine loss of consciousness.[28] This distinction is crucial because anesthetics may immobilize cephalopods without fully addressing their capacity to experience pain.

HUMANE KILLING AND WELFARE ASSESSMENT: IS HUMANE KILLING POSSIBLE?

Protocols for the killing of cephalopods clearly need refinement. Current recommendations[24] lack detailed guidelines. More work needs to be done on the validation of existing methods and the exploration of alternatives. Standardized assessments of consciousness and suffering are crucial for effectively evaluating practices as more or less humane.

THE NEED FOR BETTER WELFARE INDICATORS

The development of reliable welfare indicators for cephalopods is also needed. Current metrics often focus on health changes or physiological stress rather than directly capturing feelings.[33],[34] A comprehensive approach to assessing cephalopod welfare should include both physiological and psychological aspects. As a starting point, models used for other species, such as the welfare scoring system for Atlantic salmon[35] could be adapted for cephalopods. Current efforts to develop a "Cephalopod Welfare Index" aim to provide a more holistic welfare monitoring system.[24] Non-invasive methods, such as ultrasonography and endoscopic techniques, are emerging as tools for health assessment, though they require further refinement.[36],[37],[38] Additionally, body patterns and abnormal behaviors are being investigated as psychological parameters of welfare.[39],[40]

POSITIVE AND NEGATIVE EMOTIONS: BEYOND PAIN

Cephalopod emotions, particularly positive ones, remain under-researched. While behaviors such as play, exploration, and problem-solving have been observed,[41],[42] there is a lack of experimental testing to determine whether these behaviors are associated with positive emotions like joy, curiosity, and satisfaction.

While pain has been relatively well researched (see "Pain"), other negative feelings such as stress, fear, and boredom have been understudied. Investigating a wider range of potential negative feelings is essential for a comprehensive understanding of cephalopod emotions.

CEPHALOPOD HUSBANDRY AND REPRODUCTION

Cephalopods are cultured in captivity for various purposes including consumption, display, restocking, and scientific research.[43],[44],[45],[46] Challenges persist, particularly in the areas of nutrition and reproduction. Cephalopods are carnivorous, requiring diets composed of marine-based proteins. This reliance on marine sources poses sustainability challenges, as it can contribute to overfishing and strain on marine ecosystems. Additionally, the efficiency of converting feed into body mass (feed conversion ratio) in cephalopods is an area that requires further research to improve sustainability. Developing alternative, non-marine-based diets that meet the nutritional needs of cephalopods without compromising growth and health is an important step to making their aquaculture more sustainable. A better understanding of cephalopod digestive physiology and feeding habits will likely be needed to design more sustainable diets.[47],[48],[49],[50]

Reproductive methods also need refinement. This includes better control of sexual maturation, understanding natural factors influencing reproduction, and improving brood stock conditions. Better replicating the conditions cephalopods experience in the wild could increase their chances of reproducing successfully.[51],[52] There is also a need for greater standardization of husbandry techniques and for effective incubation methods, particularly for species like *Octopus vulgaris* that are valuable in aquaculture.[53],[45]

Enhancing our knowledge of cephalopod immune systems and disease management will be essential if we are to prevent disease outbreaks in captivity.[54],[55],[56] Implementing standardized techniques for documenting parasites and pathogens would aid in disease prevention and management. Additionally, exploring the potential use of probiotics, which have proven beneficial in other animal groups, could be valuable for cephalopods. Accordingly, identifying beneficial gut bacteria is one current research priority.[57],[58],[59]

References

1 Hanlon and Messenger 2018

2 Huffard 2013

3 a b Marini et al. 2017

4 Mather and Dickel 2017

5 a b c d Schnell, Amodio, et al. 2021

6 a b Amodio et al. 2018

7 Hochner et al. 2006

8 Hochner 2010

9 Zullo and Hochner 2011

10 Turchetti-Maia et al. 2017

11 Brown and Piscopo 2013

12 Shomrat et al. 2015

13 Amodio and Fiorito 2013

14 Jozet-Alves et al. 2013

15 Schnell, Clayton, et al. 2021

16 Schnell, Boeckle, et al. 2021

17 Darmaillacq et al. 2014

18 Jozet-Alves et al. 2023

19 Budelmann et al. 1997

20 Levy and Hochner 2017

21 Nilsson et al. 2012

22 Hank and Osorio 2018

23 Gleadall 2013

24 a b c Fiorito et al. 2015

25 Andrews and Tansey 1981

26 Gonçalves et al. 2012

27 Pugliese et al. 2016

28 a b Butler-Struben et al. 2018

29 Abbo et al. 2021

30 Miller and Leach 2015

31 Colpaert et al. 1980

32 Colpaert et al. 2001

33 Paterson and Spanoghe 1997

34 Wuertz et al. 2023

35 Stien et al. 2013

36 Tateno 1993

37 Ponte et al. 2017

38 Sykes, Almansa, et al. 2017

39 Andrade et al. 2023

40 Narshi et al. 2022

41 Poirier et al. 2004

42 Yasumuro and Ikeda 2016

43 Iglesias et al. 2014

44 Nabhitabhata and Segawa 2014

45 a b Vidal et al. 2014

46 Koueta et al. 2014

47 Nande et al. 2017

48 Linares et al. 2015

49 Gallardo et al. 2017

50 Sykes, Alves, et al. 2017

51 Cosgrove 1993

52 Garci et al. 2016

53 Iglesias et al. 2007

54 Huntingford et al. 2006

55 Ashley 2007

56 Lafferty et al. 2015

57 Balcázar et al. 2006

58 Cruz et al. 2012

59 Michael et al. 2014

Bibliography

Abbo, Lisa A., Nicole E. Himebaugh, Lindsey M. DeMelo, Roger T. Hanlon, and Robyn J. Crook. 2021. "Anesthetic Efficacy of Magnesium Chloride and Ethyl Alcohol in Temperate Octopus and Cuttlefish Species." *Journal of the American Association for Laboratory Animal Science* 60 (5): 556–567. https://doi.org/10.30802/AALAS-JAALAS-20-000076.

Amodio, Piero, Markus Boeckle, Alexandra K. Schnell, Ljerka Ostojíc, Graziano Fiorito, and Nicola S. Clayton. 2019. "Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence?" *Trends in Ecology and Evolution* 34 (1): 45–56. https://doi.org/10.1016/j.tree.2018.10.010.

Amodio, Piero, and Graziano Fiorito. 2013. "Observational and Other Types of Learning in *Octopus*." In *Invertebrate Learning and Memory,* edited by Randolf Menzel and Paul R. Benjamin. Vol. 2 of *Handbook of Behavioral Neuroscience*. Elsevier.

Andrade, Michaella P., Charles Morphy D. Santos, Mizziara M. M. De Paiva, et al. 2023. "Assessing Negative Welfare Measures for Wild Invertebrates: The Case for Octopuses." In "Invertebrate Welfare," edited by William Winlow, Jennifer A. Mather, and Anna Di Cosmo. Special issue, *Animals* 13 (19): 3021. https://doi.org/10.3390/ani13193021.

Andrews, Paul L. R., Anne-Sophie Darmaillacq, Ngaire Dennison, et al. 2013. "The Identification and Management of Pain, Suffering and Distress in Cephalopods, Including Anaesthesia, Analgesia and Humane Killing." In "Cephalopod Biology," edited by Graziano Fiorito and Giovanna Ponte. Special issue, *Journal of Experimental Marine Biology and Ecology 447* (September): 46–64. https://doi.org/10.1016/j.jembe.2013.02.010.

Andrews, Paul L. R., and E. M. Tansey. 1981. "The Effects of Some Anaesthetic Agents in *Octopus vulgaris*." *Comparative Biochemistry and Physiology Part C: Comparative Pharmacology* 70 (2): 241–247. https://doi.org/10.1016/0306-4492(81)90057-5.

Ashley, Paul J. 2007. "Fish Welfare: Current Issues in aquaculture." *Applied Animal Behaviour Science* 104 (3–4): 199–235. https://doi.org/10.1016/j.applanim.2006.09.001.

Balcázar, José Luis, Ignacio de Blas, Imanol Ruiz-Zarzuela, David Cunningham, Daniel Vendrell, and José Luis Múzquiz. 2006. "The Role of Probiotics in Aquaculture." *Veterinary Microbiology* 114 (3–4): 173–186. https://doi.org/10.1016/j.vetmic.2006.01.009.

Brown, Euan R., and Stefania Piscopo. 2013. "Synaptic Plasticity in Cephalopods: More Than Just Learning and Memory?" In "Cephalopod Biology Under the Auspices of CephRes-ONLUS," edited by Graziano Fiorito. Special issue, *Invertebrate Neuroscience* 13 (1): 35–44. https://doi.org/10.1007/s10158-013-0150-4.

Budelmann, Bernd U., Rudolf Schipp, and Sigurd von Boletzky. 1997. “Cephalopoda.” In *Mollusca II*, edited by Frederick W. Harrison and Alan J. Kohn. Vol. 6A of *Microscopic Anatomy of Invertebrates*, edited by Frederick W. Harrison. Wiley-Liss.

Butler-Struben, Hanna M., Samantha M. Brophy, Nasira A. Johnson, and Robyn J. Crook. 2018. “In Vivo Recording of Neural and Behavioral Correlates of Anesthesia Induction, Reversal, and Euthanasia in Cephalopod Molluscs.” *Frontiers in Physiology 9*:109. https://doi.org/10.3389/fphys.2018.00109.

Chappell, Bill. 2024. “Octopus Farming in the U.S. Would Be banned Under New Bill in Congress.” NPR, July 25. https://www.npr.org/2024/07/25/nx-s1-5051801/octopus-farming-ban-us-congress.

Colpaert, Francis C., Philippe De Witte, Allan N. Maroli, Frans Awouters, Carlos J. E. Niemegeers, and Paul A. J. Janssen. 1980. “Self-Administration of the Analgesic Suprofen in Arthritic Rats: Evidence of *Mycobacterium butyricum*-Induced Arthritis as an Experimental Model of Chronic Pain.” *Life Sciences* 27 (11): 921–928. https://doi.org/10.1016/0024-3205(80)90101-0.

Colpaert, Francis C., J. P. Tarayre, M. Alliaga, L. A. Bruins Slot, N. Attal, and W. Koek. 2001. “Opiate Self-Administration as a Measure of Chronic Nociceptive Pain in Arthritic Rats.” *Pain* 91 (1–2): 33–45. https://doi.org/10.1016/s0304-3959(00)00413-9.

Cosgrove, J. 1993. “In Situ Observations of Nesting Female *Octopus dofleini* (Wülker, 1910).” *Journal of Cephalopod Biology,* no. 2: 33–45.

Cruz, Patricia Martínez, Ana L. Ibáñez, Oscar A. Monroy Hermosillo, and Hugo C. Ramírez Saad. 2012. “Use of Probiotics in Aquaculture.” *International Scholarly Research Notices* 2012:916845. https://doi.org/10.5402/2012/916845.

Darmaillacq, Anne-Sophie, Ludovic Dickel, and Jennifer A. Mather, eds. 2014. *Cephalopod Cognition*. Cambridge University Press.

Di Cristina, Giulia, Paul L. R. Andrews, Giovanna Ponte, Viola Galligioni, and Graziano Fiorito. 2015. “The Impact of Directive 2010/63/EU on Cephalopod Research.” *Invertebrate Neuroscience* 15 (4): 8. https://doi.org/10.1007/s10158-015-0183-y.

Fiorito, Graziano, Andrea Affuso, Jennifer A. Basil, et al. 2015. “Guidelines for the Care and Welfare of Cephalopods in Research—a Consensus Based on an Initiative by CephRes, FELASA and the Boyd Group.” *Laboratory Animals* 49 (S2): 1–90. https://doi.org/10.1177/0023677215580006.

Gallardo, Pedro, Alberto Olivares, Rosario Martínez-Yez, et al. 2017. “Digestive Physiology of *Octopus maya* and *O. mimus*: Temporality of Digestion and Assimilation Processes.” *Frontiers in Physiology* 8:355. https://doi.org/10.3389/fphys.2017.00355.

Garci, Manuel E., Jorge Hernández-Urcera, Miguel Gilcoto, Raquel Fernández-Gago, Ángel F. González, and Ángel Guerra. 2016. "From Brooding to Hatching: New Insights from a Female *Octopus vulgaris* in the Wild." *Journal of the Marine Biological Association of the United Kingdom* 96 (6): 1341–1346. https://doi.org/10.1017/S0025315415001800.

Gleadall, Ian G. 2013. "The Effects of Prospective Anaesthetic Substances on Cephalopods: Summary of Original Data and a Brief Review of Studies over the Last Two Decades." In "Cephalopod Biology," edited by Graziano Fiorito and Giovanna Ponte. Special issue, *Journal of Experimental Marine Biology and Ecology 447* (September): 31–45. https://doi.org/10.1016/j.jembe.2013.02.008.

Gonçalves, Rui A., Cláudia Aragão, Paulo A. Frias, and António V. Sykes. 2012. "The Use of Different Anaesthetics as Welfare Promoters During Short-Term Human Manipulation of European Cuttlefish (*Sepia officinalis*) Juveniles." *Aquaculture* 370–371:130–135. https://doi.org/10.1016/j.aquaculture.2012.10.014.

Hanke, Frederike D., and Daniel C. Osorio. 2018. "Vision in Cephalopods." *Frontiers in Physiology* 9:18. https://doi.org/10.3389/fphys.2018.00018.

Hanlon, Roger T., and John B. Messenger. 2018. *Cephalopod Behaviour*. 2nd ed. Cambridge University Press.

Hochner, Binyamin, Tal Shomrat, and Graziano Fiorito. 2006. "The Octopus: A Model for a Comparative Analysis of the Evolution of Learning and Memory Mechanisms." *Biological Bulletin* 210 (3): 308–317. https://doi.org/10.2307/4134567.

Hochner, Binyamin. 2010. "Functional and Comparative Assessments of the Octopus Learning and Memory System." *Frontiers in Bioscience–Scholar* 2 (2): 764–771. https://doi.org/10.2741/S99.

Huffard, Christine L. 2013. "Cephalopod Neurobiology: An Introduction for Biologists Working in Other Model Systems." In "Cephalopod Biology Under the Auspices of CephRes-ONLUS," edited by Graziano Fiorito. Special issue, *Invertebrate Neuroscience* 13 (1): 11–18. https://doi.org/10.1007/s10158-013-0147-z.

Huntingford, F. A., C. Adams, V. A. Braithwaite. 2006. "Current Issues in Fish Welfare." *Journal of Fish Biology* 68 (2): 332–372. https://doi.org/10.1111/j.0022-1112.2006.001046.x.

Iglesias, José, Lidia Fuentes, and Roger Villanueva, eds. 2014. *Cephalopod Culture*. Springer.

Iglesias, José, F. J. Sánchez, J. G. F. Bersano, et al. 2007. "Rearing of *Octopus vulgaris* Paralarvae: Present Status, Bottlenecks and Trends." *Aquaculture* 266 (1–4): 1–15. https://doi.org/10.1016/j.aquaculture.2007.02.019.

Jozet-Alves, Christelle, Marion Bertin, and Nicola S. Clayton. 2013. "Evidence of Episodic-Like Memory in Cuttlefish." *Current Biology* 23 (23): R1033–R1035. https://doi.org/10.1016/j.cub.2013.10.021.

Jozet-Alves, Christelle, Alexandra K. Schnell, and Nicola S. Clayton. 2023. “Cephalopod Learning and Memory.” *Current Biology* 33 (20): R1091–R1095. https://doi.org/10.1016/j.cub.2023.08.013.

Koueta, Noussithé, Helene Viala, and Estelle Le Bihan. 2014. “Applications, Uses and By-products from Cephalopods.” In *Cephalopod Culture*, edited by José Iglesias, Lidia Fuentes, and Roger Villanueva. Springer.

Lafferty, Kevin D., C. Drew Harvell, Jon M. Conrad, et al. 2015. “Infectious Diseases Affect Marine Fisheries and Aquaculture Economics.” *Annual Review of Marine Science* 7:471–496. https://doi.org/10.1146/annurev-marine-010814-015646.

Levy, Guy, and Binyamin Hochner. 2017. “Embodied Organization of *Octopus vulgaris* Morphology, Vision, and Locomotion.” *Frontiers in Physiology* 8:164. https://doi.org/10.3389/fphys.2017.00164.

Linares, Marcela, Claudia Caamal-Monsreal, Alberto Olivares, et al. 2015. “Timing of Digestion, Absorption and Assimilation in Octopus Species from Tropical (*Octopus maya*) and Subtropical-Temperate (*O. mimus*) Ecosystems.” *Aquatic Biology* 24 (2): 127–140. https://doi.org/10.3354/ab00642.

Marini, Gaia, Fabio De Sio, Giovanna Ponte, and Graziano Fiorito. 2017. “Behavioral Analysis of Learning and Memory in Cephalopods.” In *Learning Theory and Behavior*, edited by Randolf Menzel. Vol. 1 of *Learning and Memory: A Comprehensive Reference*, 2nd ed., edited by John H. Byrne. Academic Press.

Mather, Jennifer A., and Ludovic Dickel. 2017. “Cephalopod Complex Cognition.” In “Comparative Cognition,” edited by Benjamin Y. Hayden and Jessica F. Cantlon. Special issue, *Current Opinion in Behavioral Sciences* 16 (August): 131–137. https://doi.org/10.1016/j.cobeha.2017.06.008.

Michael, Ekundayo Taiye, Sogbesan Olukayode Amos, and Lauratu Tahir Hussaini. 2014. “A Review on Probiotics Application in Aquaculture.” *Fisheries and Aquaculture Journal* 5 (4): 1000111. https://doi.org/10.4172/2150-3508.1000111.

Miller, Amy L., and Matthew C. Leach. 2015. “The Mouse Grimace Scale: A Clinically Useful Tool?” *PLOS ONE* 10 (9): e0136000. https://doi.org/10.1371/journal.pone.0136000.

Nabhitabhata, Jaruwat, and Susumu Segawa. 2014. “Aquaculture to Restocking.” In *Cephalopod Culture,* edited by José Iglesias, Lidia Fuentes, and Roger Villanueva. Springer.

Nande, Manuel, Pablo Presa, Álvaro Roura, Paul L. R. Andrews, and Montse Prez. 2017. “Prey Capture, Ingestion, and Digestion Dynamics of *Octopus vulgaris* Paralarvae Fed Live Zooplankton.” *Frontiers in Physiology* 8:573. https://doi.org/10.3389/fphys.2017.00573.

Narshi, Tanya M., Danielle Free, William S. M. Justice, Sarah Jayne Smith, and Sarah Wolfensohn. 2022. “Welfare Assessment of Invertebrates: Adapting the Animal Welfare Assessment Grid (AWAG) for Zoo Decapods and Cephalopods.” *Animals* 12 (13): 1675. https://doi.org/10.3390/ani12131675.

Nilsson, Dan-Eric, Eric J. Warrant, Sönke Johnsen, Roger T. Hanlon, and Nadav Shashar. 2012. “A Unique Advantage for Giant Eyes in Giant Squid.” *Current Biology* 22 (8): 683–688. https://doi.org/10.1016/j.cub.2012.02.031.

Paterson, Brian D., and Patrick T. Spanoghe. 1997. “Stress Indicators in Marine Decapod Crustaceans, with Particular Reference to the Grading of Western Rock Lobsters (*Panulirus cygnus*) During Commercial Handling.” *Marine and Freshwater Research* 48 (8): 829–834. https://doi.org/10.1071/MF97137.

Poirier, R., Raymond Chichery, and Ludovic Dickel. 2004. “Effects of Rearing Conditions on Sand Digging Efficiency in Juvenile Cuttlefish.” *Behavioural Processes* 67 (2): 273–279. https://doi.org/10.1016/j.beproc.2004.04.006.

Ponte, Giovanna, António V. Sykes, Gavan M. Cooke, Eduardo Almansa, and Paul L. R. Andrews. 2017. “The Digestive Tract of Cephalopods: Toward Non-invasive In Vivo Monitoring of Its Physiology.” *Frontiers in Physiology* 8:403. https://doi.org/10.3389/fphys.2017.00403.

Pugliese, Chiara, Rosa Mazza, Paul L. R. Andrews, Maria C. Cerra, Graziano Fiorito, and Alfonsina Gattuso. 2016. “Effect of Different Formulations of Magnesium Chloride Used As Anesthetic Agents on the Performance of the Isolated Heart of *Octopus vulgaris*.” *Frontiers in Physiology* 7:610. https://doi.org/10.3389/fphys.2016.00610.

Schnell, Alexandra K., Piero Amodio, Markus Boeckle, and Nicola S. Clayton. 2021. “How Intelligent is a Cephalopod? Lessons from Comparative Cognition.” *Biological Reviews* 96 (1): 162–178. https://doi.org/10.1111/brv.12651.

Schnell, Alexandra K., Markus Boeckle, Micaela Rivera, Nicola S. Clayton, and Roger T. Hanlon. 2021. “Cuttlefish Exert Self-Control in a Delay of Gratification Task.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1946): 20203161. https://doi.org/10.1098/rspb.2020.3161.

Schnell, Alexandra K., Nicola S. Clayton, Roger T. Hanlon, and Christelle Jozet-Alves. 2021. “Episodic-Like Memory is Preserved with Age in Cuttlefish.” *Proceedings of the Royal Society B: Biological Sciences* 288 (1957): 20211052. https://doi.org/10.1098/rspb.2021.1052.

Shomrat, Tal, Ana Turchetti-Maia, N. Stern-Mentch, Jennifer A. Basil, and Binyamin Hochner. 2015. “The Vertical Lobe of Cephalopods: An Attractive Brain Structure for Understanding the Evolution of Advanced Learning and Memory Systems.” In Invertebrate Neuroscience” edited by Alison R. Mercer and Bing Zhang. Special issue, *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology A 201* (9): 947-956. https://doi.org/10.1007/s00359-015-1023-6.

Smith, Jane A., Paul L. R. Andrews, Penny Hawkins, Susanna Louhimies, Giovanna Ponte, and Ludovic Dickel. 2013. “Cephalopod Research and EU Directive 2010/63/EU: Requirements, Impacts and Ethical review.” In “Cephalopod Biology,” edited by Graziano Fiorito and Giovanna Ponte. Special issue, *Journal of Experimental Marine Biology and Ecology 447* (September): 31–45. https://doi.org/10.1016/j.jembe.2013.02.009.

Stien, Lars H., Marc B. M. Bracke, Ole Folkedal, et al. 2013. “Salmon Welfare Index Model (SWIM 1.0): A Semantic Model for Overall Welfare Assessment of Caged Atlantic Salmon; Review of the Selected Welfare Indicators and Model Presentation.” *Reviews in Aquaculture* 5 (1): 33–57. https://doi.org/10.1111/j.1753-5131.2012.01083.x.

Sykes, António V., Eduardo Almansa, Gavan M. Cooke, Giovanna Ponte, and Paul L. R. Andrews. 2017. “The Digestive Tract of Cephalopods: A Neglected Topic of Relevance to Animal Welfare in the Laboratory and Aquaculture.” *Frontiers in Physiology* 8:492. https://doi.org/10.3389/fphys.2017.00492.

Sykes, António V., Alexandra Alves, Juan C. Capaz, et al. 2017. “Refining Tools for Studying Cuttlefish (*Sepia officinalis*) Reproduction in Captivity: In Vivo Sexual Determination, Tagging and DNA Xollection.” *Aquaculture* 479 (October 1): 13–16. https://doi.org/10.1016/j.aquaculture.2017.05.021.

Tateno, S. 1993. “Non-Invasive Analysis of Mantle Movements in *Octopus vulgaris*.” In *Recent Advances in Cephalopod Fisheries Biology: Contributed Papers to 1991 CIAC International Symposium and Proceedings of the Workshop on Age, Growth and Population Structure*, edited by Takashi Okutani, Ron K. O’Dor, and Tsunemi Kubodera. Tokai University Press.

Turchetti-Maia, Ana, Tal Shomrat, and Binyamin Hochner. 2017. “The Vertical Lobe of Cephalopods: A Brain Structure Ideal for Exploring the Mechanisms of Complex Forms of Learning and Memory.” In *The Oxford Handbook of Invertebrate Neurobiology*, edited by John H. Byrne. Oxford University Press.

Vidal, Erica A. G., Roger Villanueva, José P. Andrade, et al. 2014. “Cephalopod Culture: Current Status of Main Biological Models and Research Priorities.” In *Advances in Cephalopod Science: Biology, Ecology, Cultivation and Fisheries*, edited by Erica A. G. Vidal. *Advances in Marine Biology 67*. Academic Press.

Wuertz, Sven, David Bierbach, and Mirko Bögner. 2023. “Welfare of Decapod Crustaceans with Special Emphasis on Stress Physiology.” Aquaculture Research 2023:1307684. https://doi.org/10.1155/2023/1307684.

Yasumuro, Haruhiko, and Yuzuru Ikeda. 2016. “Environmental Enrichment Accelerates the Ontogeny of Cryptic Behavior in Pharaoh Cuttlefish (*Sepia pharaonis*).” *Zoological Science* 33 (3): 255–265. https://doi.org/10.2108/zs150197.

Zullo, Letizia, and Binyamin Hochner. 2011. “A New Perspective on the Organization of an Invertebrate Brain.” *Communicative & Integrative Biology* 4 (1): 26–29. https://doi.org/10.4161/cib.13804.

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