Cephalopoda

Chapter · February 2010

DOI: 10.1002/9781444318777.ch50

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Cephalopoda
In: *The UFAW Handbook on The Care and Management of Laboratory and Other Research Animals.*
8th Edition (Robert Hubrecht and James Kirkwood, eds). Oxford (UK): Wiley-Blackwell, pp 787-793 (2010)

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Note: This short chapter has not been written to stand on its own. It is an update of Peter Boyle's Chapter 7 in the 7th edition of the UFAW Handbook, which was published in 1999 and is reprinted after this update. Consequently, for details and earlier references the reader should consult that chapter as the authoritative text. In addition, some key literature on cephalopods published earlier (but not mentioned in that chapter) has been added. For an easy follow-up and comparison, the updates given below use (sub)headings similar to those of the earlier chapter. This chapter update is dedicated to the memory of Peter Boyle.

Introduction

Cephalopods are the only invertebrate animal group included in this edition of the Handbook, however information on decapod crustaceans is available in the 7th edition of the Handbook. Invertebrates are not generally protected in animal welfare legislation, although certain species are included in some national legislation (eg, UK, New Zealand & Australian Capital Territories, and some Scandinavian countries). The UK, at the time of writing, includes one species, *Octopus vulgaris*, in its legislation on the use of animals in research. However, there is debate within Europe (unresolved at the time of writing) as to whether some, all or no cephalopods (as well as decapod crustacea) should be included in a new European Directive on research using animals (see also Chapter 8 on legislation).

Cephalopods belong to the phylum Mollusca and thus are close relatives to gastropods and bivalves. Although the cephalopod body design conserved some typical molluscan features, it developed a level of complexity, and especially a sophisticated nervous system and sense organs, that in several aspects reach vertebrate standards (Budelmann 1995). The cephalopod nervous system is certainly the most advanced of any invertebrate nervous system and this complexity correlates well with the animals' (in general) very active, fast moving predatory life styles and sophisticated behaviours (Bullock and Horridge 1965; Budelmann 1995; Hanlon & Messenger 1996). Not surprisingly then, beginning in the 1930s with J.Z. Young's rediscovery of the giant axon and the subsequent early understanding of the processes involved in nerve impulse conduction and transmission (Adelman & Gilbert 1990), cephalopods have become fascinating and valuable invertebrate model systems for comparative vertebrate research. However, in such comparisons a number of limitations apply (see below, nervous system). It is important that these limitations should be understood because of the recent increased interest in this animal group from media and laymen that is sometimes combined with a tendency for 'over-interpretation' of the fascinating behaviours that cephalopods show.

The class Cephalopoda comprises two sub-classes: Nautiloidea (*Nautilus*) and Coleoidea (octopuses, cuttlefish and squids). The latter two are often referred to as 'decapods' but care should be taken as this term is also commonly used for the order of crustaceans that includes crabs, lobsters, prawns, etc). Nautiloids and coleoids show significant differences with regard to their anatomy, physiology and behaviour (for example, nautiluses have a much less sophisticated nervous system and sensory outfit; they show no colour change and have a much simpler behavioural repertoire; and they are scavengers and thus seem to have a well developed chemosensory system for food detection). These differences between nautiloids and coleoids, however, unfortunately are often not considered in the literature when the term 'cephalopod(s)' is applied. The term as used often refers to the coleoid cephalopods only (that is, to the octopuses, cuttlefish and squids) and, therefore, great care must be taken in the use, interpretation and generalisation of the 'cephalopod' data described.

Cephalopod biology

A number of comprehensive monographs has become available that cover almost all aspects of cephalopod biology, from palaeobiology (Landman *et al.* 1996, 2007), evolution, systematics, identification, and biogeography (Clarke 1986; Guerra 1992; Sweeney *et al.* 1992; Payne *et al.* 1998; Voss *et al.* 1998; Norman 2000; Capua 2004; Jereb & Roper 2005), to gross and microscopic anatomy (Mangold 1989; Budelmann *et al.* 1997; Nixon & Young 2003), physiology (Abbott *et al.* 1995), ecology, fisheries and culture (Boucaud-Camou 1991; Boyle & Rodhouse 2005; Chotiyaputta *et al.* 2005), age determination (Jereb *et al.* 1991), behaviour (Hanlon & Messenger 1996; Nixon & Young 2003; Borelli & Fiorito 2008) and diseases (Hanlon & Forsythe 1990; Hochberg 1990). Some more recent data are summarised below.

Habitat and distribution

An excellent monograph is now available on many aspects of cephalopod ecology and fisheries, including: cephalopod biodiversity and zoogeography; life cycle, growth and reproduction; population ecology; cephalopods as prey and predators; fishing methods and scientific sampling; fishery resources; fisheries oceanography; and assessment and management (Boyle & Rodhouse 2005).

Locomotion

The cephalopod musculature lacks a skeletal support system and, instead, operates on the principle of a muscular hydrostat, similar to the 'mechanism' of an elephant trunk or the human tongue (Kier & Smith 1985; Smith & Kier 1989). This allows cephalopod (specifically octopod) arms a great range of movement. Over the past more than 10 years, significant progress has been made in understanding the nervous control of cephalopod arm movements; this ultimately could inspire completely new strategies for the control of highly flexible robotic arms (Gutfreund *et al.* 1996, 1998; Matzner *et al.* 2000; Sumbre *et al.* 2001, 2005; Walker *et al.* 2005; Yekuteli *et al.* 2005a, 2005b, 2007).

Shell and buoyancy

The neutral buoyancy of many squids is achieved by storing ammonia in body tissue. The various mechanisms for storage (in coelomic cavities, vacuoles, or gelatinous outer layers) have been reviewed in support for the argument that ammoniacal squids have evolved as a polyphyletic animal group (Voight *et al.* 1994).

Respiration and circulation

Water temperature, pH and oxygen supply are critical factors in cephalopod culture and breeding. Recently, the cuttlefish (*Sepia officinalis*) has served as a valuable model system for understanding the mechanisms of thermal tolerance in ectothermic animals (Melzner *et al.* 2006, 2007).

Nervous system

The cephalopod nervous system is the most highly evolved of all invertebrate nervous systems. On the other hand and despite that level of complexity, the overall organisation of its central part (the brain) is fundamentally different from that of the vertebrate nervous system and, therefore, any direct comparison between the two has serious limitations. This, however, neither excludes careful comparison of basic brain functions, nor weakens the great value of the cephalopod nervous system in comparative research. Details of the anatomy of the cephalopod central nervous system are available for *Nautilus* (Young 1965), *Octopus* (Young 1971; Budelmann & Young 1985; Plän 1987) and *Loligo* (Young 1974, 1976, 1977, 1979; Messenger 1979; Budelmann & Young 1987); recent overviews are given in Budelmann (1995), Budelmann *et al.* (1997), Nixon and Young (2003) and Williamson and Chrachri (2004).

In addition to their highest level of complexity, cephalopod brains are also the largest of all the invertebrate brains; their brain:body weight ratio exceeds that of many fishes and reptiles (Packard 1972). This is not too surprising, however, since cephalopods lack an internal skeleton and lack joints, and thus lack a 'simple' antagonistic muscle control of movements. Consequently, about half of the volume of the brain of coleoid cephalopods consists of the relatively large motoneurons that form the sub-oesophageal mass of the brain; this area includes the motoneurons that expand all the chromatophore organs in the skin (for a summary of the numbers of nerve cells in the various parts of the *Octopus* brain, see Budelmann 1995). On the other hand, the comparatively large size and complexity of the brains of octopuses, cuttlefish and squids are the basis for the animals' large repertoire of fascinating behaviours, including various forms of learning and short- and long-term memory (Hanlon & Messenger 1996; Hochner *et al.* 2003; Borelli & Fiorito 2008). Ultimately, these make coleoid cephalopods, especially shallow-water octopods, cuttlefish and squids, the only invertebrate species with which humans can directly interact ('communicate') in a back and forth manner and beyond a simple reflex-like (re)action on the animals' side.

Octopuses, cuttlefish and squids are often considered the most 'intelligent' invertebrate species (whichever way intelligence is defined). The web-based Wikipedia summarises this issue quite well:

> *Cephalopod intelligence has an important comparative aspect in our understanding of intelligence, because it relies on a nervous system fundamentally different from that of vertebrates. ... The scope of cephalopod intelligence is controversial ... Classical conditioning of cephalopods has been reported, and one study (Fiorito and Scotto 1992) even concluded that octopuses practice observational learning. However, the latter idea is strongly disputed, and doubt has been shed on some other reported capabilities as well. In any case, impressive spatial learning capacity, navigational abilities, and predatory techniques remain beyond question.*

Other impressive behaviours that can be added to this list are cephalopod mating and social behaviours, including social recognition (Hanlon & Messenger 1996; Boal *et al.* 2000; Dickel *et al.* 2000; Karson *et al.* 2003; Boal 2006; Alves *et al.* 2008; Borelli & Fiorito 2008).

Powerful techniques have now successfully been applied to cephalopod brains to the study of their anatomy and function (Budelmann *et al.* 1995): three-dimensional magnetic resonance imaging of brain pathways (Quast *et al.* 2001) and individual neurons (Gozansky *et al.* 2003); brain slice recordings (Williamson & Budelmann 1991); recordings from intact animals with implanted electrodes (Bullock & Budelmann 1991); and mapping of metabolic brain activity (Novicki *et al.* 1992). With these modern neurophysiological techniques cephalopods have become an increasingly valuable invertebrate model system for comparative vertebrate research, such as the evolution of learning and memory and other higher brain functions (Hochner *et al.* 2006). Recently, laterality in the brain (Byrne *et al.* 2002, 2004, 2006), play behaviour (Kuba *et al.* 2006), personality (Sinn & Moltschaniwskyj 2005), sleep (Brown *et al.* 2006) and complex phenomena, such as consciousness and suffering in cephalopods, have been discussed (Mather 2001, 2008).

Sense organs

Cephalopods have a sophisticated sensory outfit that includes all major sense organs, such as photoreceptors (including extra-ocular photoreceptors), distance and contact chemoreceptors, and various mechanoreceptors (including equilibrium receptor organs, a lateral line analogue system and a neck proprioceptive organ) (Budelmann 1996). Knowledge about touch, pressure and muscle proprioceptors is limited, and it still remains to be seen whether cephalopods have electroreceptors and are sensitive to pain. For a comprehensive summary on cephalopod sense organs, see Budelmann *et al.* (1997).

Eyes and vision

The cephalopod and vertebrate lens eyes are a textbook example of analogy (convergent evolution) between an invertebrate and a vertebrate sensory system. Recent advances have been made in understanding visual processing (Chrachri & Williamson 2003, 2004, 2005; Chrachri *et al.* 2005; Douglas *et al.* 2005), and the role of polarised vision (Saidel *et al.* 1983; Shashar *et al.* 1998, 2002; Boal *et al.* 2004; Saidel *et al.* 2005; Mäthger & Hanlon 2006). In addition, in the squid *Lolliguncula* a dorsal light reflex has been described (Preuss & Budelmann 1995a) and in cuttlefish a countershading reflex (Ferguson *et al.* 1994).

Equilibrium receptor organs

A tremendous body of data has accumulated over the past 40 years on the anatomy, ultrastructure and physiology of the cephalopod equilibrium receptor organs (statocysts), which include sophisticated receptor systems for the detection of linear (gravity) and angular accelerations (Budelmann *et al.* 1987; for summaries, see Budelmann 1990; Budelmann *et al.* 1997; for the *Nautilus* statocyst, see Neumeister & Budelmann 1997). Special emphasis has been paid to the similarities between the structure and function of the cephalopod and vertebrate hair cells (eg, Budelmann & Williamson 1994; Budelmann 2000), including their ion channels and efferent innervation (Williamson 1995) and transmitter and transmitter-like substances; the latter include nitric oxide (Tu & Budelmann 2000) and cannabinoids (Tu & Budelmann, unpublished). Cephalopod statocysts are known to drive a sophisticated control system for compensatory eye movements; part of its central organisation resembles that of the vertebrate vestibulo-oculomotor reflex pathway and involves four (*Nautilus*), seven (octopods), or 13–14 (cuttlefish and squids) extra-ocular eye muscles (Budelmann & Young 1984, 1993; Neumeister & Budelmann 1997).

Epidermal lines

The epidermal lines (formerly known as 'Drüsenlinien') that occur on the head and arms of at least some of the coleoid species are analogous to the fish and aquatic amphibian lateral line systems (Budelmann & Bleckmann 1988; Budelmann *et al.* 1997).

Neck proprioceptive organ

Similar to the vertebrate neck muscle proprioceptors, cuttlefish and squid have groups of epidermal hair cells on their neck that serve as a proprioceptive neck organ for the control of the position of the head relative to the body (Preuss & Budelmann 1995b).

Vibration receptors and hearing

Cephalopods are sensitive to vibrational stimuli via statocyst receptors and sense local water movements with their lateral line analogue system (Budelmann & Bleckmann 1988; Williamson 1988; Packard *et al.* 1990; Bleckmann *et al.* 1991; Komak *et al.* 2005). On the other hand, there is much confusion regarding cephalopods ability to 'hear'. Ultimately, this is a semantic issue since the answer depends on the definition of underwater sound and underwater hearing (Budelmann 1992). In conventional terms, cephalopods cannot hear because they do not have a receptor system that is specialised for the detection of the pressure wave of underwater sound.

Maintenance, culture and laboratory procedures

With the growing interest in cephalopods for research and commercial mariculture, as well as their popularity in public and private displays, knowledge about the maintenance, culture and proper laboratory procedures is of increased importance (Oestmann *et al.* 1997; Sykes *et al.* 2006; Dunlop & King 2008). For advice on optimising the survival of hatchling cuttlefish and squid, see Forsythe *et al.* (1994), Vidal *et al.* (2002a, 2002b) and Sykes *et al.* (2003). With regard to culture density, recent cuttlefish data show that lower stocking density results in better growth (Domingues *et al.* 2003; Correia *et al.* 2005), as does higher water temperature (25°C compared to 17°C; Forsythe *et al.* 2002). On the other hand, lower temperature (15°C compared to 27°C) extends the life cycle (Domingues *et al.* 2002). For the development of memory in cuttlefish, an enriched environment is crucial during their second and/or third months of life (Dickel *et al.* 2000). Crowding of adult cuttlefish should be avoided since it stimulates aggression (Boal *et al.* 1999).

Not surprisingly, the quality and composition of food has been proven to be critical for good growth and survival. Adult cuttlefish show much better growth rates when fed with live or thawed natural prey than when fed with an artificial diet (Domingues *et al.* 2005). Shrimp-based food pellets, although less palatable, produce maintenance growth, whereas a highly palatable fish-based surimi diet (mimicking the meat of lobster, crab and other shellfish) results in poor survival (Castro *et al.* 1993). When fed with live mysid shrimp, grass shrimp, or fish fry, young cuttlefish showed best growth during the first week after hatching when fed with mysid shrimp, and thereafter when fed with grass shrimp; cuttlefish fed with fish fry showed lowest growth rates at all times (Domingues *et al.* 2004). When prey is maintained for feeding juvenile cuttlefish, prey starvation should be avoided (Correia *et al.* 2009). Although *Sepia* shows an innate food preference, early familiarisation with other food can override this preference (Darmaillacq *et al.* 2006). For the importance of certain elements (including copper and strontium) in the food of octopus, cuttlefish and squid, see Koueta *et al.* (2002) Villanueva and Bustamente (2006) and Iglesias *et al.* (2007).

A comprehensive monograph is now available on invertebrate medicine that includes a chapter on cephalopods (Lewbart 2006) and ethical and welfare considerations for working with cephalopods have recently been summarised (Mather & Anderson 2007; Moltschaniwskyj *et al.* 2007).

Occupational health hazards

Many octopus and, particularly, cuttlefish and squid species may bite, specifically when stressed, disturbed or improperly handled. Their sharp, parrot-like beaks can inflict significant wounds and the saliva can have a variety of toxic effects. The tetrodotoxin-like venom of the Australian blue-ringed octopod (*Hapalochlaena maculosa*) can be lethal to humans (Williamson *et al.* 1996, for a review).

Cannibalism

Cannibalism is well known in octopuses, cuttlefish and squids when held in captivity. Obvious reasons include a too high stocking density and an inadequate amount of food and shelter. Specifically, when food supply is limited and feeding *ad libitum* becomes a problem, larger animals may prey upon smaller ones when kept is the same tank. In addition, sexual cannibalism has been described in an octopus species on a coral reef (Hanlon & Forsythe 2008).

Autophagy

Some data (other than anecdotal) are now available on autophagy (self eating) in *Octopus vulgaris.* They suggest that it is caused by either a substance that is released by the animals themselves or, more likely, by viruses or bacteria; stress may contribute to this behaviour but does not seem to be its primary cause (Budelmann 1998).

Further information and reading

A large number of references to the literature on cephalopods are available from the library service of the Smithsonian Institution Research Information System at http://sirismm.si.edu/siris/siris-cephalopod.htm.

The following web pages provide very useful information regarding all major aspects of cephalopod biology, supply and maintenance, rearing, culture and breeding and laboratory procedures (with regard to the scientific accuracy, however, general caution must be taken because of its lack of peer review):

Tree of Life – Cephalopods: http://tolweb.org/cephalopoda
Association of Zoos & Aquariums: http://www.aza.org
The Cephalopod Page: http://www.thecephalopodpage.org
The National Resource Center for Cephalopods: http://www.cephalopod.org
Cephbase: http://www.cephbase.com
The Octopus News Magazine Online: http://www.tonmo.com

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