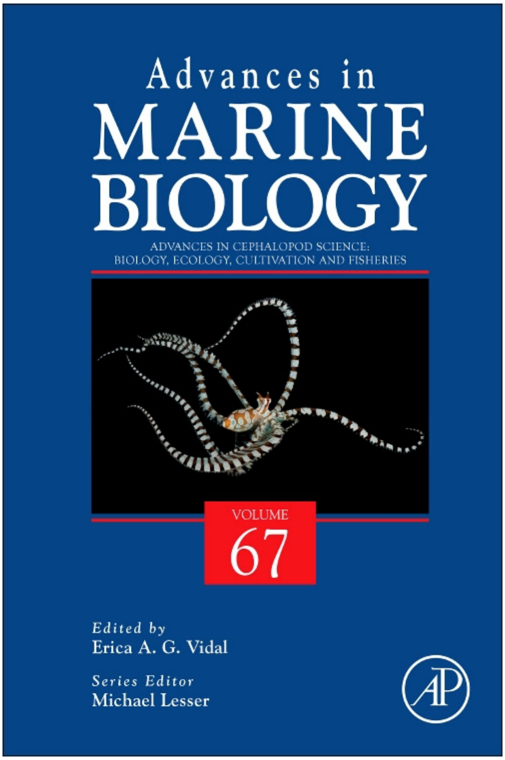

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CHAPTER THREE

The Study of Deep-Sea Cephalopods

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Abstract

"Deep-sea" cephalopods are here defined as cephalopods that spend a significant part of their life cycles outside the euphotic zone. In this chapter, the state of knowledge in several aspects of deep-sea cephalopod research are summarized, including information sources for these animals, diversity and general biogeography and life cycles, including reproduction. Recommendations are made for addressing some of the remaining knowledge deficiencies using a variety of traditional and more recently developed methods. The types of oceanic gear that are suitable for collecting cephalopod specimens and images are reviewed. Many groups of deep-sea cephalopods require taxonomic reviews, ideally based on both morphological and molecular characters. Museum collections play a vital role in these revisions, and novel (molecular) techniques may facilitate new use of old museum specimens. Fundamental life-cycle parameters remain unknown for many species; techniques developed for neritic species that could potentially be applied to deep-sea cephalopods are discussed. Reproductive tactics and strategies in deep-sea cephalopods are very diverse and call for comparative evolutionary and experimental studies, but even in the twenty-first century, mature individuals are still unknown for many species. New insights into diet and trophic position have begun to reveal a more diverse range of feeding strategies than the typically voracious predatory lifestyle known for many cephalopods. Regular standardized deep-sea cephalopod surveys are necessary to provide insight into temporal changes in oceanic cephalopod populations and to forecast, verify and monitor the impacts of global marine changes and human impacts on these populations.

Keywords: Cephalopoda, Deep sea, Diversity, Collection methods, Reproduction, Longevity, Trophic ecology, Evolution, Biogeography

1. INTRODUCTION

The deep sea, comprising both the sea floor and the overlying water column below the photic zone, is the largest and least-known environment of the Earth. According to recent calculations, less than 0.0001% of the deep-sea floor has been investigated, and even less for the deep pelagic (Ramirez-Llodra et al., 2010), yet 32 of the 33 known phyla of plants and animals are found in the oceans (most with representatives in the deep sea), and 15 of these are exclusively marine (Beaumont et al., 2006), and most of these have representatives in the deep sea. This chapter focuses on one particular class of Mollusca: the cephalopods, which form an important and fascinating component of this vast but unexplored environment.

Although the cephalopod families inhabiting the oceanic and deep-sea environments are numerous (42 of the 50 known families), they tend to be less speciose than coastal families (Young et al., 1998). Cephalopods occur not only in a wide range of deep-sea habitats, for example, seamounts, open water and continental slopes, but also in extreme environments such as hydrothermal vents and oxygen minimum zones (e.g. Clarke, 2008; Gilly et al., 2013; Ramirez-Llodra et al., 2010; Roeleveld et al., 1992; Roper and Young, 1975; Voight, 2000). Cephalopod body forms throughout these waters vary widely (Figures 3.1 and 3.2); squids range in size from small pyroteuthids of several grams to giants and colossals (e.g. *Mesonychoteuthis hamiltoni* Robson, 1925) weighing up to 500 kg (Jereb and Roper, 2010) and from gelatinous drifters (e.g. Bolitaenidae) to swift, agile hunters (e.g. Gonatidae). Deep-sea octopod sizes at maturity also range from just a few hundred grams (e.g. *Bathypolypus arcticus* Prosch, 1849, O'Dor and Malacaster, 1983) to an impressive 75 kg for *Haliphron atlanticus* Steenstrup, 1861 (O'Shea, 2004b). Habitat usage is similarly diverse; while most deep-sea squid species are pelagic and most octopods benthic, examples of each group can be found from the midwater down to or near the sea floor.

Many oceanic cephalopod species, especially squids, have wide geographical ranges. Given their broad distribution patterns and the large volume of their habitat, these oceanic squids are likely to form the bulk of the worldwide deep-sea cephalopod biomass, similarly to what has been shown for midwater fishes (Irigoien et al., 2014). It is therefore not surprising that pelagic cephalopods are among the dominant prey items for many valuable commercial fish species (e.g. tunas and billfishes) and are very important in the diets of many endangered marine animals like whales, seals and sharks (e.g. Clarke, 1996; Klages, 1996; Smale, 1996). The few studies that estimate the abundance of deep-sea squids suggest enormous population sizes and biomass—for example, sperm whales alone have been estimated to consume more than 110 million tonnes of oceanic squids annually (Clarke, 1977a), which considerably exceeds the annual total capture of marine and freshwater organisms harvested by humans (90 million tonnes) (FAO, 2012).

Given that some cephalopod species appear to have cosmopolitan distributions, while others are restricted to narrow geographical ranges, it is not surprising that understanding the systematics of deep-sea taxa in particular remains a work in progress. Specimens of many deep-sea species remain rare

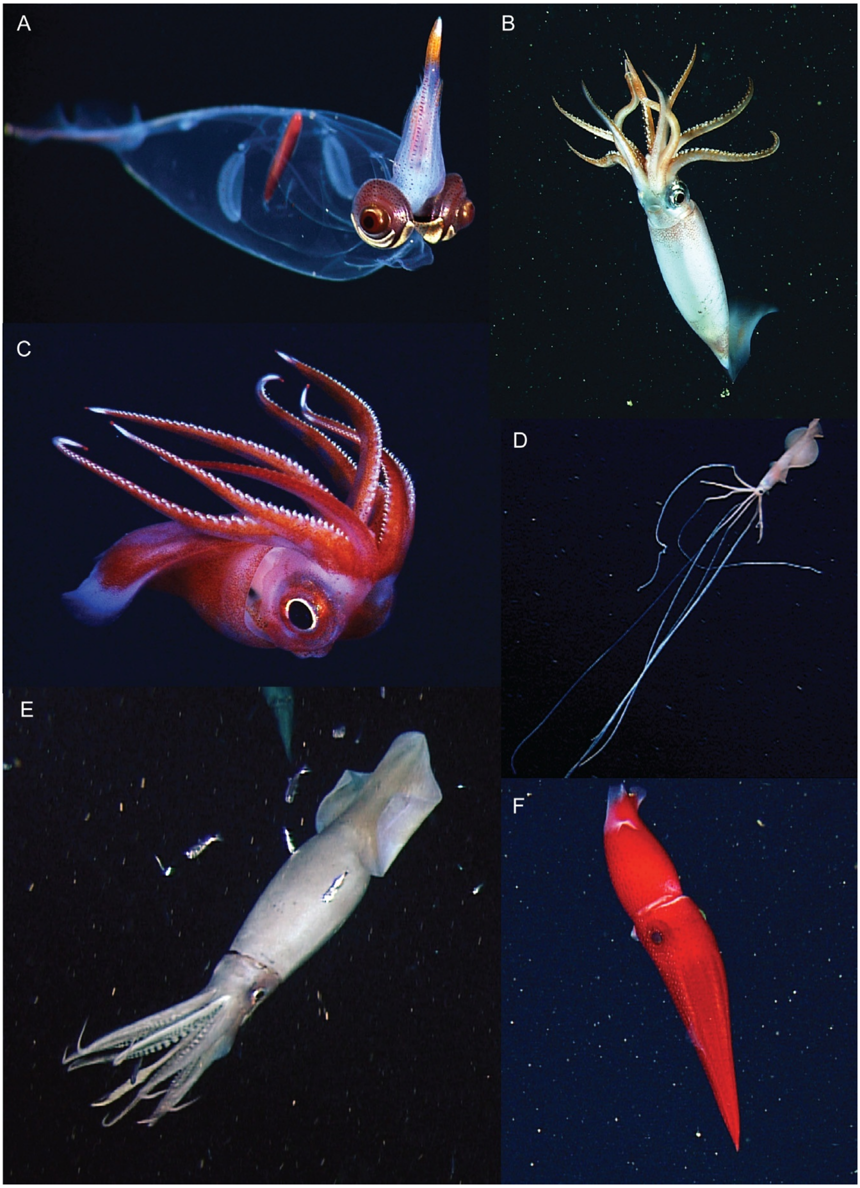

Figure 3.1 Examples of deep-sea squids as observed by the ROV programme of the Monterey Bay Aquarium Research Institute. (A) *Galiteuthis phyllura*. (B) *Octopoteuthis deletron*. (C) *Dosidicus gigas*. (D) *Gonatus* sp. (E) *Magnapinna* sp. (F) *Histioteuthis heteropsis*. *(A) © 2009 MBARI. (B) © 2008 MBARI. (C) © 2006 MBARI. (D) © 2001 MBARI. (E) © 2009 MBARI. (F) © 2011 MBARI.*

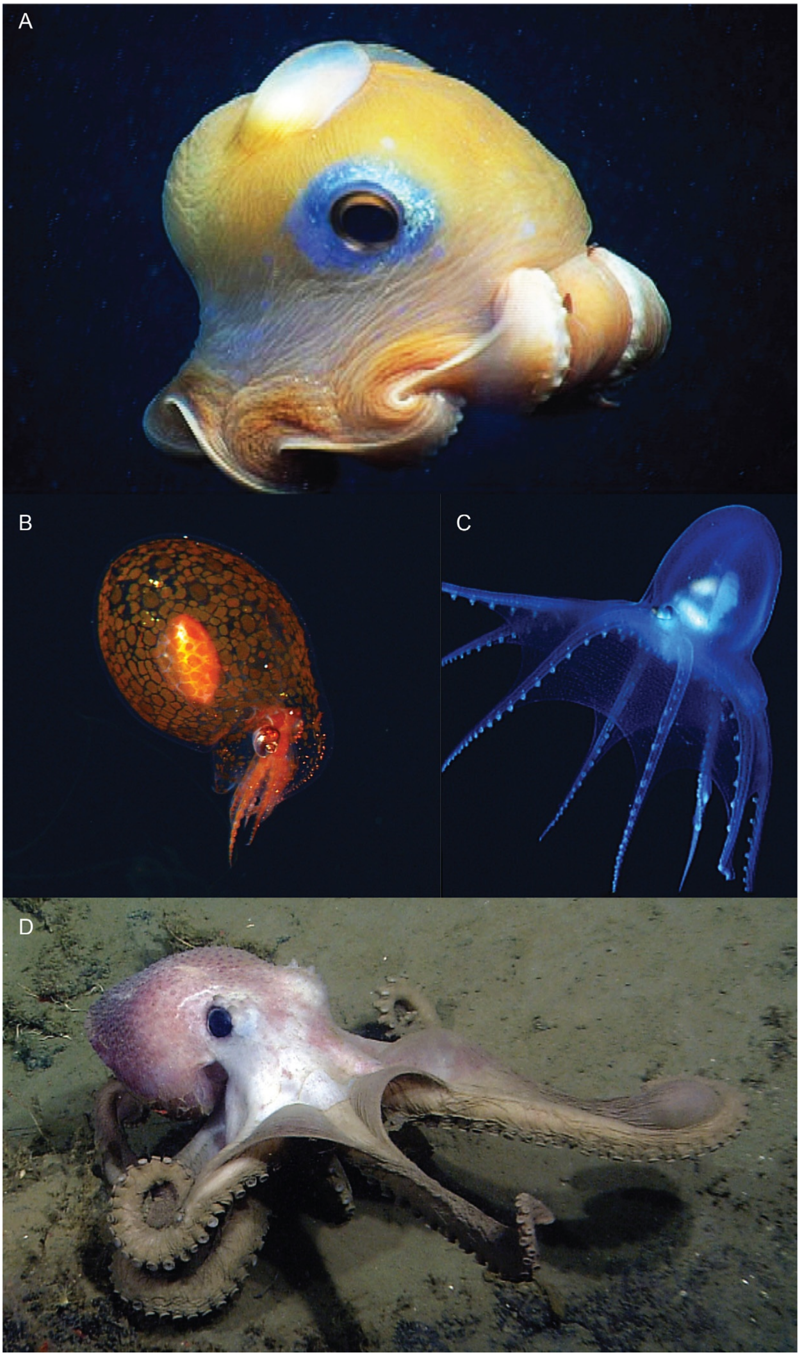

Figure 3.2 Examples of deep-sea octopods as observed by the ROV program of the Monterey Bay Aquarium Research Institute. (A) *Opisthoteuthidae*. (B) *Bolitaenidae*. (C) *Vitreledonella richardi*. (D) *Graneledone*. *(A) © 1999 MBARI. (B) © 2009 MBARI. (C) © 2001 MBARI. (D) © 2007 MBARI.*

in collections, with specimens in suitable condition to permit detailed morphological descriptions in comparison even rarer. Fresh tissue for molecular study is likewise difficult to obtain, so meaningful comparison among taxa and even entire faunas from different geographical region can be quite challenging.

Taxonomy aside, in many squid families such as Histioteuthidae ("jeweled" or "violet" squids) and Cranchiidae ("glass" squids), which are abundant in the diets of cetaceans (e.g. Clarke, 1996), even basic biological knowledge, such as information on age and size at sexual maturity remains unknown for many species. By contrast, the muscular ommastrephid squids (another cephalopod family consumed by cetaceans and comprising 10% of all known oceanic squid species) are relatively well studied (e.g. Rosa et al., 2013a), partly because they form the bulk of all globally fished cephalopods (Caddy and Rodhouse, 1998). While some ommastrephid species primarily inhabit euphotic waters, others migrate regularly into the deep sea. However, their life-history traits (being strong, agile hunters and voracious carnivores, with high growth rates and life cycles of about 1 year) are not necessarily representative of most deep-sea squids and cannot always be used to infer information about lesser known oceanic cephalopods.

Although our knowledge of the life cycle of most oceanic and deep-sea cephalopods is still very limited and built upon generalizations (often from relatively few species), the current understanding of the coleoid cephalopod life cycle is that these animals grow quickly and have relatively short life cycles and die after a single period of reproduction (semelparity) (e.g. Boyle and Rodhouse, 2005). However, accumulating evidence indicates a diversity of semelparous reproductive strategies (Hoving, 2008; Laptikhovsky et al., 2007; Rocha et al., 2001); for example, some species spawn a single egg mass, while others produce several over a period of time. The limited timespan of the cephalopod life and reproductive cycles must heavily influence the development and optimization of the single reproductive cycle. An increasing body of evidence does suggest that the life cycles of deeper-living cephalopods are longer than those of shallow-dwelling species (e.g. Arkhipkin, 1997; Hoving and Lipinski, 2009; Laptikhovsky, 2013; Seibel et al., 2005), but evidence is still lacking for most taxa. Existing knowledge on longevity in deep-sea cephalopods will therefore be reviewed, and available techniques to determine the ages of individual cephalopods will be discussed.

It has been argued that the semelparous life-history strategy requires a highly opportunistic lifestyle, where prey from a wide variety of organisms is taken, often in large amounts, to fuel the energetic costs associated with semelparity and nektonic lifestyle (Rodhouse and Nigmatullin, 1996). It is not surprising that such cephalopods (e.g. families Gonatidae and Ommastrephidae) are insatiable carnivores (Rodhouse and Nigmatullin, 1996). Unfortunately, despite the importance of oceanic and deep-sea cephalopods in marine food webs, data on their diets, feeding strategies and trophic positions are scarce. Recent developments show, however, that the typical "voracious, versatile predatory" feeding strategy (sensu Rodhouse and Nigmatullin, 1996) does not apply to all cephalopods. For example, vampire squids (*Vampyroteuthis infernalis* Chun, 1903) squids have recently been reported to ingest a wide variety of food including detritus (Hoving and Robison, 2012). Since the publication of Rodhouse and Nigmatullin's (1996) comprehensive review, new information has been collected for a wider variety of cephalopods, including oceanic and deep-sea species. New techniques have also provided more detailed insight into the trophic position and temporal feeding variability of a number of species (e.g. Cherel and Hobson, 2005; Jackson et al., 2007; Phillips et al., 2003a,b). For this chapter, literature published since 1996 has been prioritized in order to summarize and describe new information on dietary analysis and the feeding strategies and trophic positions of deep-sea cephalopods.

The primary reason for the absence of general biological knowledge on many deep-sea cephalopods is the inaccessibility of their environment. The first worldwide study of oceanography was carried out during 1872–1876 by the British naval vessel HMS *Challenger*. The best equipment of the day—nets, trawls, dredges, submarine thermometers, instruments to collect sediment samples, and copious quantities of rope—were used to collect vast amounts of information and thousands of specimens that are still being studied today. Some specimens came from depths as great as 5700 m in the Pacific, providing the first evidence that life was indeed to be found in the deep sea. Many new cephalopod species were collected on this expedition, including several deep-sea taxa (Hoyle, 1886) (Figure 3.3).

The collection of deep-sea organisms remains expensive because it requires dedicated expeditions and specialized gear. In addition, oceanic and deep-sea cephalopods are difficult to catch. Being highly mobile and visually attuned animals, some squids are able to avoid many types of oceanographic gear. As a result, there can be considerable differences between the composition of trawl catches and what is found among stomach contents of predators (which are generally capable of capturing large and sexually mature individuals, while human collection methods tend to miss these life stages) (Clarke, 1977b; Rodhouse, 1990; Xavier et al., 2003a). However, when dedicated deep-sea expeditions are able to deploy a wide variety of gear, they may provide a wealth of specimens and information on deep-sea cephalopods. A good example of a successful twenty-first-century expedition to sample cephalopods with traditional gears and modern techniques was been the MAR-ECO cruise of the Norwegian R/V *G.O. Sars* to the Mid-Atlantic Ridge in 2004 (Vecchione et al., 2010b). During this expedition, which formed part of the Census of Marine Life project (Vecchione et al., 2010c), a total number of 1295 cephalopods were caught, representing 56 species of which the majority were oceanic and deep-sea species.

Continuing application development of modern ocean-sampling technology (such as ROVs, manned submersibles and autonomous camera systems) for deep-sea exploration has provided many new insights into the biology and ecology of poorly known deep-sea cephalopods (e.g. Bush et al., 2009; Hoving and Robison, 2012; Kubodera and Mori, 2005; Kubodera et al., 2007; Seibel et al., 2005; Vecchione et al., 2001; Widder, 2013). Spectacular high-definition imagery (even 3D) is now available for species that were previously only known from mangled net-captured specimens. Footage of these animals often (understandably) captures the attention of the general public. Deep-sea cephalopods are charismatic and publications on new behaviour or other discoveries are increasingly covered as news items. Therefore, they may function as emblematic organisms for deep-sea conservation efforts (e.g. *Architeuthis dux* Steenstrup, 1860, and Guerra et al., 2011).

In the recent years, evidence has increasingly shown that populations of (oceanic) cephalopods may respond to or be impacted by changes in the marine environment and human activities including oceanic warming, expanding hypoxia and fishing (Gilly et al., 2013; Golikov et al., 2013; Rodhouse, 2013; Zeidberg and Robison, 2007). Indeed, cephalopods in general have been described as good climate-change indicators (Pecl and Jackson, 2008), and the degree of plasticity some coastal and oceanic species show in their life-history strategies under different oceanographic regimes suggests that they may be preadapted for climate change (Hoving et al., 2013a; Pecl and Jackson, 2008; Rodhouse, 2013). In areas of overexploitation of commercial fish stocks, increases in cephalopod populations have been reported (Caddy and Rodhouse, 1998; Vecchione et al., 2009a; Zeidberg and Robison, 2007). On the other hand, deeper-living, less mobile cephalopods with low metabolic rates (e.g. *Histioteuthis* spp.;

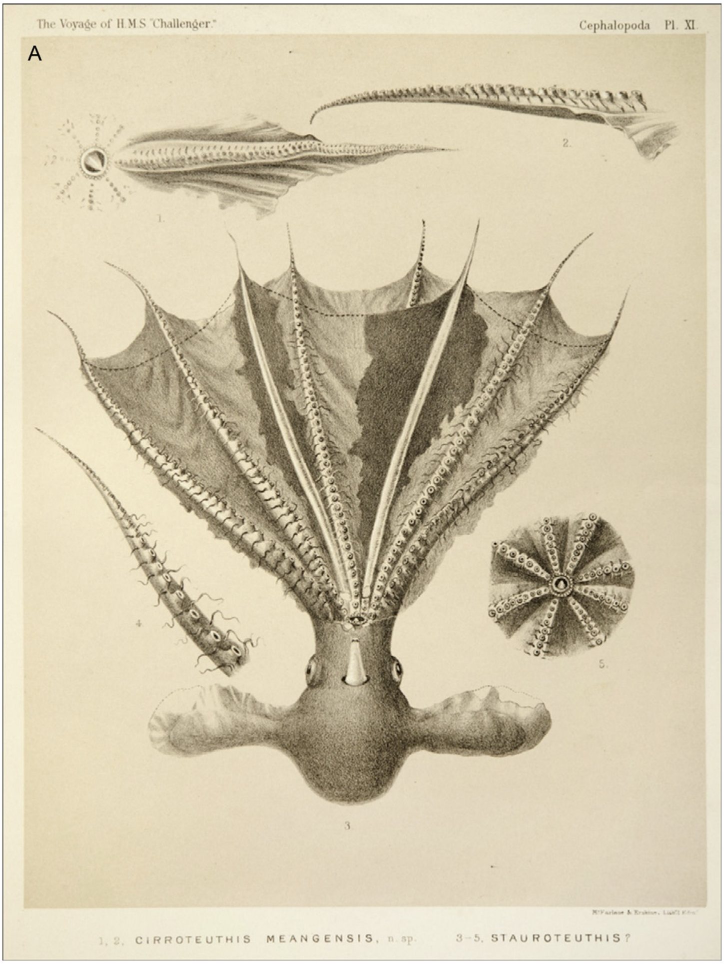

Figure 3.3 (A) Many new deep-sea species were collected during the voyage of the HMS *Challenger* during the years 1873–1876. These are copies of some of the plates from the expedition report (Hoyle, 1886). (A) Plate XI, figs. 1–2, arms of *Cirroteuthis magna* n. sp. (now *Cirrothauma magna*, (Hoyle, 1885)); figs. 3–5, *Stauroteuthis ?*, ventral view of animal (3), distal arm tip (4), and oral view of arm crown (5).

Octopoteuthis deletron Young, 1972; and *Japetella diaphana* Hoyle, 1885; Seibel et al., 1997) may be less able to cope with environmental changes than some of the more opportunistic and adaptable teuthoids. Overall, very little baseline data on life cycles, distribution, diversity, and abundance are available to assist in understanding or predicting the potential responses of deep-sea cephalopods to global marine stressors and change.

Figure 3.3—Cont'd (B) Plate XII, *Cirroteuthis magna* n. sp. (now *Cirrothauma magna* (Hoyle, 1885)); lateral view of animal (1), distal tip of arm (2), lateral view of right dorsal arm (3), middle of arm (4), centre of arm crown (5), upper beak (6) and lower beak (7).

Because of the discrepancy between the increasing awareness of deep-sea cephalopods' importance and the poor status of our general knowledge on their diversity, biology, and ecology, and our limited ability to collect them, a workshop was held during the Cephalopod International Advisory Council meeting in Florianópolis, Brazil, in October–November 2012. This chapter aims to summarize the discussions that took place, to synthesize what is currently known and to identify knowledge gaps about deep-sea cephalopods. More specifically, we aim to summarize and discuss

- a working definition of a "deep-sea cephalopod";
- the varied sources of information on deep-sea cephalopods that are available;
- the current state of (and gaps in) knowledge on cephalopod diversity, biogeography, evolution, life cycles (i.e. reproduction and longevity) and trophic ecology;
- deep-sea cephalopod populations in the context of ocean change.

We hope that this chapter will enable future researchers studying these animals to better integrate the disparate data collection methods available and to continue to improve worldwide understanding of these important, charismatic residents of the world's largest habitat.

2. WHAT IS A "DEEP-SEA" CEPHALOPOD?

The deep sea is generally defined as the volume of water beneath the euphotic zone. In most environments, this is below 200 m, while in some tropical oligotrophic waters, light may penetrate into ocean layers as deep as 300 m. The deepest unbiased benthic cephalopod record in the literature is a cirrate octopus that was photographed at 5145 m off Barbados (Jahn, 1971). The deepest unbiased record of a squid to date is a "bigfin" squid (Magnapinnidae) observed at 4735 m by DSV *Nautile* in the western Atlantic off Brazil (Vecchione et al., 2001).

One of the difficulties in classifying cephalopods based on their depth distribution is that cephalopods may have quite extreme vertical distributional ranges. For example, *Dosidicus gigas* (d'Orbigny, 1835) commonly ranges from near-surface waters (<25 m, e.g. during nocturnal hunting) to mesopelagic oxygen minimum zones (e.g. Gilly et al., 2006) and has been recorded down to 1447 m (Stewart et al., 2013).

Many other cephalopods migrate from deep waters (below 200 m) up to epipelagic waters at night (e.g. Piatkowski et al., 1994; Roper and Young, 1975; Watanabe et al., 2006). Some cephalopods may occupy different depths during particular phases of their life cycles; the young of many deep-sea cephalopod species spend part of their early lives in epipelagic waters and undergo ontogenetic descent as they grow and mature (e.g. Quetglas et al., 2010; Rodhouse and Piatkowski, 1995; Roper and Young, 1975; Young, 1978).

Therefore dwelling or utilizing the volume outside the euphotic zone for "a significant portion of the life cycle" may constitute a single contiguous period early or late in the life cycle (ontogenetic descent/ascent), or a contiguous proportion of each day (diel vertical migration), or regular but brief forays into deep waters (e.g. diving to hunt). When considering which cephalopods should be treated as "deep-sea" groups, it is important to note that, while this designation can be made at high taxonomic levels in some cases (e.g. the order Vampyromorpha), in others, it may vary among genera within a family or even congeneric species. While cuttlefish are generally considered a coastal, shallow-dwelling group, some species of the genus *Sepia* do occur at great depth (Reid, 2001). Nautiluses are found in tropical locations, where the euphotic zone extends to greater depths, but they have also been reported from true deep-sea strata (Young, 2010). Octopods are more challenging to categorize. Although some species have been well studied and their depth ranges appear reasonably clear (e.g. *Vitreledonella richardi* Joubin, 1918) (Clarke and Lu, 1975; Lu and Clarke, 1975), the combination of taxonomic instability and sparse distribution records leaves others (e.g. *Grimpoteuthis* spp.) with the vague habitat estimate of "benthic," sometimes with a hypothetical depth range. While similar uncertainty also surrounds the exact depth ranges of some squids, in many squid genera, the majority (if not all species) reside below the euphotic zone at some life stage. It appears rare for a squid family to have a mix of deep-dwelling and exclusively shallow-dwelling genera; typically, one deep-sea genus within a family indicates that all other confamilial groups inhabit the deep sea as well. Some notably abundant families with "true" deep-sea members (species that live the majority of their lives below the euphotic zone) are Cranchiidae, Histioteuthidae, Octopoteuthidae, and the "chiroteuthid" families (which contain Chiroteuthidae, Mastigoteuthidae, Joubiniteuthidae, Magnapinnidae, Promachoteuthidae and Batoteuthidae); however, many other families are widely represented in this environment. The onychoteuthids should also be considered important in this category; while little is known about their vertical distribution, and they are often classified as being a "midwater" family of squid (Lefkaditou et al., 2000), specimens have been recorded from depths of over 1200 m (Bolstad, 2010).

Several recent deep-sea observations have suggested that an improved understanding of reproductive strategies could also help characterize species that should be considered "deep-sea" cephalopods. To date, the majority of pelagic squid eggs and egg masses have been found in epipelagic waters, suggesting that squids such as those of the relatively well-reported families

Enoploteuthidae, Ommastrephidae and Thysanoteuthidae, utilize the epipelagic zone for reproduction. However, too little is known about pelagic egg masses from other squid families to assume that all squids that produce egg masses reproduce in the epipelagic zone. Deep-sea squids like Architeuthidae and Octopoteuthidae are also likely to produce egg masses as suggested from their asynchronous ovulation (Hoving et al., 2004, 2008a). Brooding squids have been observed in the deep sea (Bush et al., 2012; Seibel et al., 2005) but also in the epipelagic zone (*Gonatus madokai* Kubodera and Okutani, 1977) (Bower et al., 2012). While additional observations on cephalopod reproductive biology in the deep sea may eventually enable further habitat-use inferences to be drawn across taxa, the body of information presently available on egg masses and spawning in oceanic cephalopods seems insufficient to divide cephalopods into deep-sea species and non-deep-sea species based solely on reproductive strategy.

> *For this chapter, a deep-sea cephalopod is one that depends on the deep-ocean environment (defined as below the euphotic zone) for a significant part of its life cycle*

This working definition is not perfect as it may include some oceanic cephalopods that spawn or spend a large part of the day in epipelagic waters (e.g. Ommastrephidae, Enoploteuthidae and Thysanoteuthidae). However, these species do also depend on the deep sea for a significant part of the day and are therefore included in this chapter. This inclusion allows for comparison among species and families. In several other animal groups, recent information indicates that many animals traditionally categorized as "shallow-water" or "epipelagic" also utilize the deep sea; examples include tiger sharks (Werry et al., 2014), several tuna species (e.g. Block et al., 2001), leatherback sea turtles (Houghton et al., 2008) and emperor penguins (Zimmer et al., 2010). Thus, it appears that, among highly mobile macrofauna, it is not uncommon to range through multiple depth zones even when usually associated with euphotic waters.

In terms of "usual" residents, the neritic zone and deep sea, although comprising quite different physical environments, are thought to contain similar numbers of cephalopod species. However, the genera represented differ greatly between the two environments. According to Young et al. (1998), around 70% of the cephalopod families found in the oceanic pelagic zone are oegopsids, in contrast to neritic environments, which are dominated by myopsid squids, Sepioidea, and incirrate octopods. In fact, cirrate octopods, vampyromorphs and most oegopsid squids (except ommastrephids and enoploteuthids) are rarely found in euphotic waters during their lives, although some oegopsids (e.g. members of the family Cranchiidae) are known to live in euphotic waters during early life phases (Arkhipkin, 1996b,c; Bolstad et al., 2014; Voss, 1985). The results of Young et al. (1998) show two contrasting groups of animals, with little overlap, living in the neritic and oceanic zones of the ocean. Cephalopod taxa represented in the deep sea are outlined in Table 3.1, with references for supporting evidence for their inclusion. Given that 42 cephalopod families (12 families of Octopoda, 29 families of Decapodiformes and the family Nautilidae) are represented in this habitat, it is important to expand our understanding of those cephalopods living at depth.

3. INFORMATION SOURCES FOR DEEP-SEA CEPHALOPODS

Cephalopods are conspicuous components of the deep-sea biota, with some dwelling in the benthic boundary layer (e.g. mastigoteuthid squids and cirrate octopods) and deep pelagic ocean throughout their entire life cycles. Some cephalopods (including *Architeuthis*, some cirrates and some cranchiids) are among the largest species of the deep sea. Early reports of deep-sea cephalopods were often derived from findings of floating or stranded carcasses and the few specimens collected during early expeditions. These reports progressively increased as a growing number of specimens were found in the stomach contents of large deep-sea-feeding predators (e.g. oceanic toothed whales) or captured by commercial and scientific nets (e.g. Clarke, 1980, 1996, 2006; Santos et al., 1999). Morphological and taxonomic analyses of such specimens not only enabled a broader comprehension of the diversity of deep-sea cephalopod forms but also raised many important questions regarding their life histories, behaviour, physiology, abundance, distribution and functional roles in deep-sea communities. These questions were difficult to address due to the shortcomings and relative rarity of available samplers, only sampling a minute fraction of the vast spaces of the deep sea (Herring, 2002). Moreover, because specimens were brought lifeless to the surface (or were partially digested remains), little could be inferred about the lives of these cephalopods.

Modern underwater samplers and optical and acoustic technologies developed to explore the deep sea have not yet fully solved the problem of quantitative sampling of cephalopods. However, optical tools have finally

Table 3.1 Generic and specific diversity of each cephalopod family (alphabetical by order and family)

Order	Family	Known genera	Known species	Revisionary taxonomic works	Deep-sea genera	Depth range sources
Cirrate Octopoda	Cirroctopodidae*	1	4		*Cirroctopus*	Vecchione et al. (2008a,b)
	Cirroteuthidae*	3	6	Guerra et al. (1998); Collins and Henriques (2000)	*Cirroteuthis* *Cirrothauma* *Stauroteuthis*	Vecchione et al. (2008a,b) Vecchione et al. (2008a,b) Collins et al. (2008)
	Grimpoteuthidae*	3	19		*Cryptoteuthis* *Grimpoteuthis* *Luteuthis*	Vecchione et al. (2008a,b)
	Opisthoteuthidae*	1	20		*Opisthoteuthis*	Vecchione et al. (2008a,b)
Incirrate Octopoda	Alloposidae*	1	2		*Haliphron*	Young (2013)
	Amphitretidae*	5	11		*Amphitretus* *Bolitaena* *Japetella* *Vitreledonella*	Young et al. (2013) Young (2008) Young (2008) Young et al. (2010)
	Argonautidae	1	4			
	Bathypolypodidae*	1	7		*Bathypolypus*	Quetglas et al. (2001)
	Eledonidae	2	7	Rochebrune (1884c), Kubodera and Okutani (1994)		
	Enteroctopodidae*	3	11		*Muusoctopus* *Vulcanoctopus*	Kemp et al. (2006) González et al. (1998)

Continued

Table 3.1 Generic and specific diversity of each cephalopod family (alphabetical by order and family)—cont'd

Order	Family	Known genera	Known species	Revisionary taxonomic works	Deep-sea genera	Depth range sources
	Megaleledonidae*	12	40	Lu and Stranks (1994), Allcock et al. (2004), Allcock (2005)	*Graneledone*	Voight (2000)
	Octopodidae*	25	172	Norman et al. (2005), Gleadall (2013)	*Octopus*	Hochberg et al. (2009)
	Ocythoidae	1	1			
	Tremoctopodidae*	1	4	Thomas (1977)	*Tremoctopus*	Mangold et al. (2010)
Myopsida	Australiteuthidae	1	1			
	Loliginidae	11	47	Blainville (1823), Naef (1912a,b), Lu et al. (1985), Borri et al. (1986), Alexeyev (1992), Brakoniecki (1996), Vecchione et al. (1998a)		
Nautilida	Nautilidae*	2	6		*Nautilus*	Young (2010)
Oegopsida	Ancistrocheiridae*	1	1		*Ancistrocheirus*	
	Architeuthidae*	1	1	Winkelmann et al. (2013)	*Architeuthis*	
	Batoteuthidae*	1	1		*Batoteuthis*	Guerra et al. (2012)

Brachioteuthidae*	2	7		*Brachioteuthis* *Slosarczykovia*	Lipinski and Young (2008) Lipinski (2001)
Chiroteuthidae*	4	19		*Asperoteuthis* *Chiroteuthis* *Grimalditeuthis* *Planctoteuthis*	Young and Roper (2011a) Roper and Young (2013) Young and Roper (2011b) Vecchione et al. (2008a,b)
Cranchiidae*	13	60	Nesis (1972, 1974), Voss (1980)	*Bathothauma* *Cranchia* *Egea* *Galiteuthis* *Helicocranchia* *Leachia* *Liguriella* *Liocranchia* *Megalocranchia* *Mesonychoteuthis* *Sandalops* *Taonius* *Teuthowenia*	Young and Mangold (2009) and Voss (1980) Voss (1980) Voss (1980) Voss (1980) Young and Mangold (2008) Voss (1980) Voss (1980) Voss (1980) Voss (1980) Voss (1980) Young and Mangold (1996) and Voss (1980) Young and Mangold (2011) and Voss (1980) Young and Mangold (2010)
Cycloteuthidae*	2	4	Young and Roper (1969)	*Cycloteuthis* *Discoteuthis*	Young (2012a) Young (2012a)

Continued

Table 3.1 Generic and specific diversity of each cephalopod family (alphabetical by order and family)—cont'd

Order	Family	Known genera	Known species	Revisionary taxonomic works	Deep-sea genera	Depth range sources
	Enoploteuthidae*	4	43	Nesis (1978, 1987b) and Tsuchiya and Okutani (1998)	*Abralia*	Tsuchiya and Young (2008)
					Abraliopsis	Tsuchiya and Young (2008)
					Enoploteuthis	Tsuchiya and Young (2008)
					Watasenia	Tsuchiya and Young (2008)
	Gonatidae*	4	19		*Berryteuthis*	Kubodera et al. (2013)
					Eogonatus	Kubodera et al. (2013)
					Gonatopsis	Kubodera et al. (2013)
					Gonatus	Kubodera et al. (2013)
	Histioteuthidae*	2	19	Voss (1969) and Voss et al. (1998)	*Histioteuthis*	Horstkotte (2008)
					Stigmatoteuthis	Young and Vecchione (2007)
	Joubiniteuthidae*	1	1		*Joubiniteuthis*	Young (2009)
	Lepidoteuthidae*	1	1	Nesis and Nikitina (1990)	*Lepidoteuthis*	Young and Vecchione (2012)
	Lycoteuthidae*	4	6	Arocha (2003)	*Lampadioteuthis*	Vecchione and Young (1999)
					Lycoteuthis	Vecchione and Young (1999)
					Nematolampas	Vecchione and Young (1999)
					Selenoteuthis	Vecchione and Young (1999)
	Magnapinnidae*	1	3		*Magnapinna*	Vecchione and Young (2013)

	Mastigoteuthidae*	5	~17	Braid et al. (2013)	*Echinoteuthis* *Idioteuthis* *Magnoteuthis* *Mastigopsis* *Mastigoteuthis*	Braid (2013) Vecchione et al. (2007)
	Neoteuthidae*	4	4		*Alluroteuthis* *Narrowteuthis* *Neoteuthis* *Nototeuthis*	Young et al. (1999) Young and Vecchione (2005) Vecchione and Young (2003a) Vecchione and Young (2003b)
	Octopoteuthidae*	2	9	Clarke (1967), Stephen (1985)	*Octopoteuthis* *Taningia*	Young and Vecchione (2013a) Vecchione et al. (2010a)
	Ommastrephidae*	11	20	Nigmatullin (1992), Dunning (1998), Dunning and Förch (1998), Dunning and Wormuth (1998), Roper et al. (1998)	*Dosidicus* *Eucleoteuthis* *Hyaloteuthis* *Illex* *Nototodarus* *Ommastrephes* *Ornithoteuthis* *Sthenoteuthis* *Todarodes* *Todaropsis*	Young and Vecchione (2013b) Watanabe et al. (2006) Young and Vecchione (2010b) Vecchione and Young (2011) Stark (2008) Young and Vecchione (2009) Vecchione and Roper (1991) Moiseev (1991) Quetglas et al. (1998) Clarke (1966)

Continued

Table 3.1 Generic and specific diversity of each cephalopod family (alphabetical by order and family)—cont'd

Order	Family	Known genera	Known species	Revisionary taxonomic works	Deep-sea genera	Depth range sources
	Onychoteuthidae*	7	25	Kubodera et al. (1998), Nesis (2000), Bolstad (2010)	*Ancistroteuthis*	Bolstad (2010)
					Callimachus	Bolstad (2010)
					Filippovia	Bolstad et al. (2010)
					Kondakovia	Bolstad (2010)
					Notonykia	Bolstad (2010)
					Onychoteuthis	Bolstad (2010)
					Onykia	Bolstad (2010)
	Pholidoteuthidae*	1	2		*Pholidoteuthis*	Vecchione and Young (2012)
	Promachoteuthidae*	1	3	Roper and Young (1968)	*Promachoteuthis*	Young and Vecchione (2003)
	Psychroteuthidae*	1	1		*Psychroteuthis*	Piatkowski (2011)
	Pyroteuthidae*	2	6		*Pterygioteuthis*	Lindgren et al. (2013)
					Pyroteuthis	Lindgren et al. (2013)
	Thysanoteuthidae*	1	1		*Thysanoteuthis*	Young and Vecchione (2010c)
	Walvisteuthidae	1	1	Nesis et al. (1998)	*Walvisteuthis*	
Sepiida	Sepiadariidae	2	8	Steenstrup (1881)		
	Sepiidae*	3	114	Rochebrune (1884b), Adam (1944), Adam and Rees (1966), Khromov (1987a,b), Khromov et al. (1998), and Lu (1998) [Australia]	*Sepia*	Reid et al. (2005)

	Sepiolidae*	16	70	Joubin (1902), Naef (1912b,c,e), and Berry (1921, 1932)	*Amphorateuthis*	Young et al. (2007)
					Choneteuthis	Lu and Boucher-Rodoni (2006)
					Heteroteuthis	Young et al. (2008a,b)
					Iridoteuthis	Young et al. (2007)
					Nectoteuthis	Young et al. (2007)
					Neorossia	Reid et al. (2005)
					Rossia	Reid et al. (2005)
					Sepiolina	Young et al. (2007)
					Sepioloidea	Reid (2009)
					Stoloteuthis	Young et al. (2007)
Spirulida	Spirulidae*	1	1		*Spirula*	Young (2012b)
Vampyromorpha	Vampyroteuthidae*	1	1		*Vampyroteuthis*	Young (2012c)
(Unassigned) Decapodiformes	Bathyteuthidae*	1	3	Rochebrune (1884a), Roper (1969)	*Bathyteuthis*	Roper (2012)
	Chtenopterygidae*	1	4		*Chtenopteryx*	Young and Vecchione (2010a)
	Idiosepiidae	1	8			
Total	50	174	845			

Families containing deep-sea species are indicated by an asterisk, and those most in need of focused taxonomic revision are highlighted (grey). Data were obtained from WoRMs (WoRMS Editorial Board, 2014), valid taxa were selected (only full genera and species, not subgenera or subspecies) and those that had not been validated by a taxonomic editor were checked individually. For the Octopoda, the recent revised classification of Strugnell et al. (2013) has been followed. Revisionary taxonomic works refer to taxa (either families or genera) that have been revised on the basis of their worldwide representatives and not restricted to a particular geographical area.

allowed live observations in natural habitats (e.g. Kubodera et al., 2007), tracking of active movements with high spatial and temporal resolution (Benoit-Bird and Gilly, 2012), and even live or essentially intact collection (e.g. Robison et al., 2003). These tools, combined with the development of a range of molecular and biochemical techniques, have expanded the scale of scientific approaches to address unanswered questions and have raised new intriguing questions (some of which are described in this chapter). Thus, the information available on deep-sea cephalopods today originates from a variety of sources and serves different purposes. The basic types of records that can be obtained from cephalopods in the deep sea and the information each can potentially produce are summarized in Table 3.2. Additional information can be gained by combining data from multiple sources. For example, the capture of a number of specimens in a defined area of known habitats, geographical positions and depths may provide specimens for a variety of studies in addition to distribution and abundance records. The value of these diverse records for cephalopod and deep-sea scientific research and other purposes, including assessment of human impacts, conservation and society demands, is addressed in Table 3.3.

3.1. Types of gear: Advantages and disadvantages

Diverse methods are useful for obtaining specimens and/or images of cephalopods in the deep sea. Every deep-sea specimen, photo, or video is potentially a valuable source of information about the species, whether revealing aspects of its life history, genetics, biochemical adaptations, role in the food web or other characteristics. However, each sampling method has its own set of problems, especially for quantitative inferences such as distribution and abundance. Logistical considerations, such as size and capability of ships necessary to deploy the gear and distance to the study area, are also important controlling factors in these deep-sea studies. It is important to remember that each of the gear types discussed in the succeeding text is most effective for only a component of the cephalopod assemblage. The greater the variety of gear that can be included in a study, the more completely and confidently inferences can be made about the total cephalopod fauna (Vecchione et al., 2010b). For example, bottom trawling may collect animals on relatively flat substrates, while baited cameras can attract scavengers in rough terrain or midwater, and submersibles can be used to search for animals that are not attracted to bait, in nontrawlable areas.

Table 3.2 Types of deep-sea cephalopod records and the potential information available from each

Record		Description	Potential information
Organism	Specimen	Individuals brought to surface dead in variable body condition, including body parts	Macro- and microscopic body morphology and morphometrics. If fresh, tissue samples for genetic and biochemical analyses. Potential source of stomach contents, statoliths, gladii, beaks
	Live	Specimens of any deep-sea cephalopod brought to surface alive and potentially fit to live in captivity for some period of time	As for specimens plus observations of live morphology, anatomical structure function and behaviour in captivity. Measurements of physiological processes and experimentation
Observational information	Live animals	Video or still images of live individuals in nature	Observations of natural morphology (e.g. posture, colour) behaviour and other individual characters in nature
		Video or still images of live individuals in aquaria	
	Contextual	Video or still images of deep-sea habitats that contain cephalopod specimens and potentially other organisms	As for specimen images but also observation of natural habitats and species interactions
Abundance records	Species	Numbers or biomass of cephalopod species in a specific area or water volume	Relative abundance indices. Temporal evidence of distribution patterns, e.g. diel or longer-term migrations
	Community	Diversity or biomass of cephalopod species and other organisms in a specific area or water volume	Relative indices of multiple species of a deep-sea community

Continued

Table 3.2 Types of deep-sea cephalopod records and the potential information available from each—cont'd

Record		Description	Potential information
Spatial records	Depth	Cephalopod specimens' position in relation to the sea surface and/or the sea floor (altitude)	Evidence of vertical distribution, movements (e.g. diel, ontogenetic) and habitats (pelagic, benthopelagic)
	Horizontal	Cephalopod specimens' geographical position (latitude, longitude)	Evidence of geographical (horizontal) distribution and movements

3.1.1 Nets and longlines

Many net designs are available, each of which samples only a portion of the total fauna (e.g. Wenneck et al., 2008). Effective sampling of the three-dimensional pelagic environment, with its temporal variability, requires different gear from studies focusing on epibenthic animals. Both pelagic and benthic gear include some nets for which the mouth opening is set by a rigid frame and others for which the mouth shape is determined by hydrodynamic forces.

3.1.1.1 Rigid-frame nets

Rigid-frame epibenthic trawls, such as beam trawls and the Agassiz trawl, have a long history of successful deep-sea sampling (Thistle, 2003). Because they can be fished on a single relatively light wire and because they orient right side up when they contact the bottom, deploying them is relatively simple and winch requirements are modest—a single level-wind winch that will hold enough wire for a scope of at least 3 × the target depth. Such nets have collected important octopod specimens (Vecchione et al., 2005). Rigid-frame epibenthic trawls are available in various sizes but none are wide enough to sweep a broad area like, for example "otter trawl", a double-warp otter trawl can. Generally, the height of the mouth opening is much less than that of an otter trawl. The results of these height/width constraints are both positive and negative. Although the area (or volume) sampled by the rigid-frame net can be calculated with relative confidence, the reduced size of the mouth opening greatly reduces the efficiency of the gear for sampling highly mobile animals like cephalopods.

Many different rigid-frame pelagic nets have been used to collect cephalopods. Examples include bongo nets, Isaacs–Kidd midwater trawls (IKMT), Tucker trawls, rectangular midwater trawls (RMT) (Clarke,

Table 3.3 Value of different types of deep-sea cephalopod records for various scientific applications

	Organism		Images		Abundance		Spatial records	
	Specimen	Live	Live Animals	Contextual	Species	Community	Depth	Horizontal
Cephalopod research								
Taxonomy—systematics	■	■	▒	▒	░	░	▒	▒
Phylogeny—evolution	■	▒	░	░	░	░	░	░
Life histories	■	■	■	■	░	░	■	■
Population dynamics	■	░	░	░	■	░	▒	▒
Physiology	▒	■	■	▒	░	░	▒	▒
Behaviour	░	■	■	■	░	░	■	■
Abundance	▒	░	▒	▒	■	▒	▒	▒
Distribution	■	░	■	■	▒	▒	■	■
Feeding	■	■	■	■	░	░	▒	▒
Predators	░	░	░	▒	░	░	░	░
Deep-sea research								
Habitat description	░	░	░	■	░	░	▒	▒
Biodiversity (richness)	■	░	▒	■	░	░	▒	▒
Community structure	■	░	▒	■	▒	■	▒	▒
Energy flow (food chains)	■	▒	░	▒	░	░	▒	▒
Biogeography	■	░	■	■	▒	▒	■	■
Deep-sea adaptations	■	■	■	■	░	░	▒	░
Human impacts and conservation								
Fishery assessment	░	░	▒	▒	■	■	▒	▒
Fishery impacts	■	░	■	■	■	■	■	■
Oil/mining impacts	■	▒	▒	■	▒	▒	■	■
Global changes	■	▒	■	■	■	■	■	■
Deep-sea conservation	■	░	■	■	▒	▒	■	■

Continued

Table 3.3 Value of different types of deep-sea cephalopod records for various scientific applications—cont'd

	Organism		**Images**		**Abundance**		**Spatial records**	
	Specimen	**Live**	**Live Animals**	**Contextual**	**Species**	**Community**	**Depth**	**Horizontal**
Societal needs								
Deep-sea public awareness	▒	▒	▓	▓	░	░	░	▒
Education	▒	▒	▓	▓	░	░	▒	▒
Arts—entertainment	▒	▒	▓	▓	░	░	░	▒

Very useful ▓

Useful ▒

Indifferent ░

1977b) and multiple opening/closing nets with environmental sampling system (MOCNESS) (Wiebe et al., 1985). Frame shape and size determine fishing characteristics and mesh size determines what is retained in the cod end. Small nets designed for zooplankton sampling can be effective for collecting paralarvae. The larger rigid-frame gear is generally appropriate for micronekton (e.g. adults of small species such as pyroteuthids, enoploteuthids and juveniles of larger species, such as cranchiids, chiroteuthids and pelagic octopods) (Wiebe et al., 1985). Rigid-frame pelagic nets may be configured to be fished open throughout the tow or rigged so that the net opens and closes at specific depths or times. Although the open configuration is easier to fish, opening/closing nets must be used in order to infer depth distributions with any confidence. A simple mechanical opening/closing device can be effective for targeting a layer or avoiding surface contamination, but multiple samples require multiple deployments, each of which uses precious ship time. Multiple net samplers, such as the RMT and MOCNESS, were therefore developed for determining vertical distributions and migratory patterns. Acoustic triggers and timers can be used for multiple samples during a single deployment. However, the methods that are most effective use conducting cable to send opening and closing signals and can at the same time transmit environmental data such as temperature, pressure (to calculate depth) and conductivity (for salinity).

3.1.1.2 Larger trawls

Nets for which shape is determined by hydrodynamics (e.g. otter trawls) can be much larger than rigid-frame nets and can therefore sample much larger specimens. These types of gear are the best source of adult cephalopods but catch a surprising number of smaller specimens as well. These nets are often similar to gear used in shallow water for fisheries studies but, when used for deep-water nekton, must be rigged with deep-water floats capable of withstanding great pressure. They are effective for sweeping a larger area of the bottom or filtering a larger volume in midwater studies than the rigid-frame nets. The epibenthic versions are usually made of more robust components (heavier trawl doors and bridles, stronger twine, headropes and footropes, etc.) than the pelagic nets. Both epibenthic and pelagic nets can be fished on either a single or a double warp, the latter requiring a much more specialized ship with two large-capacity trawling winches capable of holding great lengths of heavy wire with sophisticated winch-control systems. Few ships exist with such capabilities: larger fisheries research ships such as *G.O. Sars* (Norway) and long-range commercial trawlers are examples. Although the single-warp gear can be fished from a less-specialized ship and is easier to deploy and recover, the double-warp gear can be much larger, again increasing sampled area/volume and capturing larger specimens. It is noteworthy that, because epibenthic trawls are open during deployment and recovery, they sometimes collect important midwater specimens on the way down or back up (e.g. *Magnapinna* sp. A in Vecchione et al., 2010b).

Some otter trawls have uniform mesh size in all parts of the net (e.g. the Norwegian "krill trawl"), but typically, the large nets use graded mesh sizes from as much as 2 m in the wings of the net to just a few millimetres in the cod end. When sampling cephalopods, it is extremely important to search the large mesh carefully as the net, either pelagic or epibenthic, is being retrieved onto the ship. Often, most of the cephalopods are entangled in the large mesh and must be picked by hand before the net is stored on the net reel. This requires careful coordination between the deck crew and the science party.

Pelagic trawls can be rigged with multiple opening/closing cod ends for quasi-discrete depth sampling. However, because just the cod end of the net is opened and closed rather than the entire net, the likelihood of contamination of the sample with specimens that entered the net prior to opening of the cod end is greater than with a rigid-frame net. Another alternative configuration used especially for pelagic sampling is a hard (or "aquarium") cod end that protects the sample from abrasion or crushing. Although this is very useful for obtaining specimens in good condition for some taxa (e.g. fishes and gelatinous megaplankton), it is less useful for cephalopods because of their tendency to entangle in the mesh of the net. Thermally protected cod ends have also been developed; these facilitate recovery of living deep-sea organisms (Childress et al., 1978). Various net sensors can be rigged on the trawl, either using acoustic sensors on the gear itself or using a third wire system. However, the farther the gear is from the ship, the more problematic these sensor configurations become; this is especially troublesome for deep-sea sampling with multi-kilometre depths and wire scope of 2–3 × the depth.

3.1.1.3 Passive collecting gear

Another type of net that has been successfully used in the epipelagic to catch large squids that may migrate vertically into the deep sea during the day, such as ommastrephids and onychoteuthids, is entangling ("gill") nets. The effectiveness of such nets when deployed in the deep sea remains to be seen. Jigging can also be an effective method for catching large vertical migrators (e.g. ommastrephids).

Long lines with many baited hooks are sometimes used in the deep sea both commercially and for research. Although the typical catch of such long lines is almost entirely fishes, sometimes large cephalopods, such as *Ommastrephes bartramii* (Lesueur, 1821), *Mesonychoteuthis hamiltoni* and *Architeuthis dux* are also hooked (M. Vecchione, personal observation). Even recovery of a broken-off tentacle can yield an important tissue sample for DNA and other biochemical analyses (e.g. Kubodera and Mori, 2005; Robison, 1989).

Other baited devices sometimes attract cephalopods as well. The "bait" may be traditional organic bait or some other type of attractant, such as light. The first *in situ* observations of the giant squid (*Architeuthis*) and also of *Taningia danae* Joubin, 1931, were obtained with organic bait (Kubodera et al., 2005) and organic bait and light, respectively (Kubodera et al., 2007). Light traps use a general light source, but recently, lures have been developed that attempt to mimic bioluminescent patterns generated by deep-sea animals. Such a lure, based on the "burglar alarm" bioluminescence signal of a particular medusa, was recently used to obtain the first *in situ* video record of a giant squid, *Architeuthis* (Widder, 2013). A similar lure attracted a large deep-sea squid that could not be identified confidently to any known family (Widder, 2007). The objective of the device using bait or lure may be to catch specimens (a trap) or record photographic or video records (a camera lander). Typically, these devices are deployed by the ship or submersible and left for some period while the ship pursues other objectives. For example, incirrate octopods have been attracted to baited benthic landers that take photos periodically over a period of many hours (Kemp et al., 2006). Similar baited camera systems have been used in midwater layers by lowering the system on a cable from a ship (e.g. Kubodera et al., 2005, 2007).

3.1.2 Submersibles and related in situ *mechanisms*

While nets provide samples that integrate distribution over a relatively large area, they are less effective for inferring small-scale distribution or behaviour. Methods based on visual observations are much better for addressing these types of questions. The simplest of these methods are "drop cameras" lowered from a ship to an area of interest. More hydrodynamic camera sleds can also be towed behind a ship. Both drop cameras and camera sleds can be used for video but typically record still images at predetermined intervals, providing semirandom snapshot observations of the target area. Neither observation method collects specimens, which is often an important corroboration tool for confident identification.

Better control and selective targeting of specific fauna, both epibenthic and pelagic, can be achieved by use of submersibles, either manned or unmanned (Robison, 2000, 2004). Although the relative value of manned submersibles versus remotely operated vehicles has been the subject of considerable debate, both have been quite useful for increasing our knowledge of deep-sea cephalopods (e.g. Bush et al., 2009; Hoving and Vecchione, 2012; Robison et al., 2003; Seibel et al., 2005; Vecchione and Roper, 1991). Both manned and unmanned submersibles can record high-quality videos and still images and can search areas not accessible to methods like net sampling. Both can also be configured to collect specimens using suction devices, detritus (or "D") samplers (first developed by Harbor Branch Oceanographic Institution) (essentially large tube segments that can be manoeuvred around an animal in midwater and then closed at both ends) (Figure 3.4b–d) and manipulator arms. While nets can collect many more specimens, these are generally not in very good condition. Specimens collected by submersible are often in excellent condition, with delicate features intact, and many are alive when brought into the laboratory aboard the ship. It has even been possible using such specimens to perform experiments and physiological measurements on deep-sea cephalopods and collect behavioural observations (e.g. Hoving and Robison, 2012; Hunt, 1996; Jacoby et al., 2009; Robison

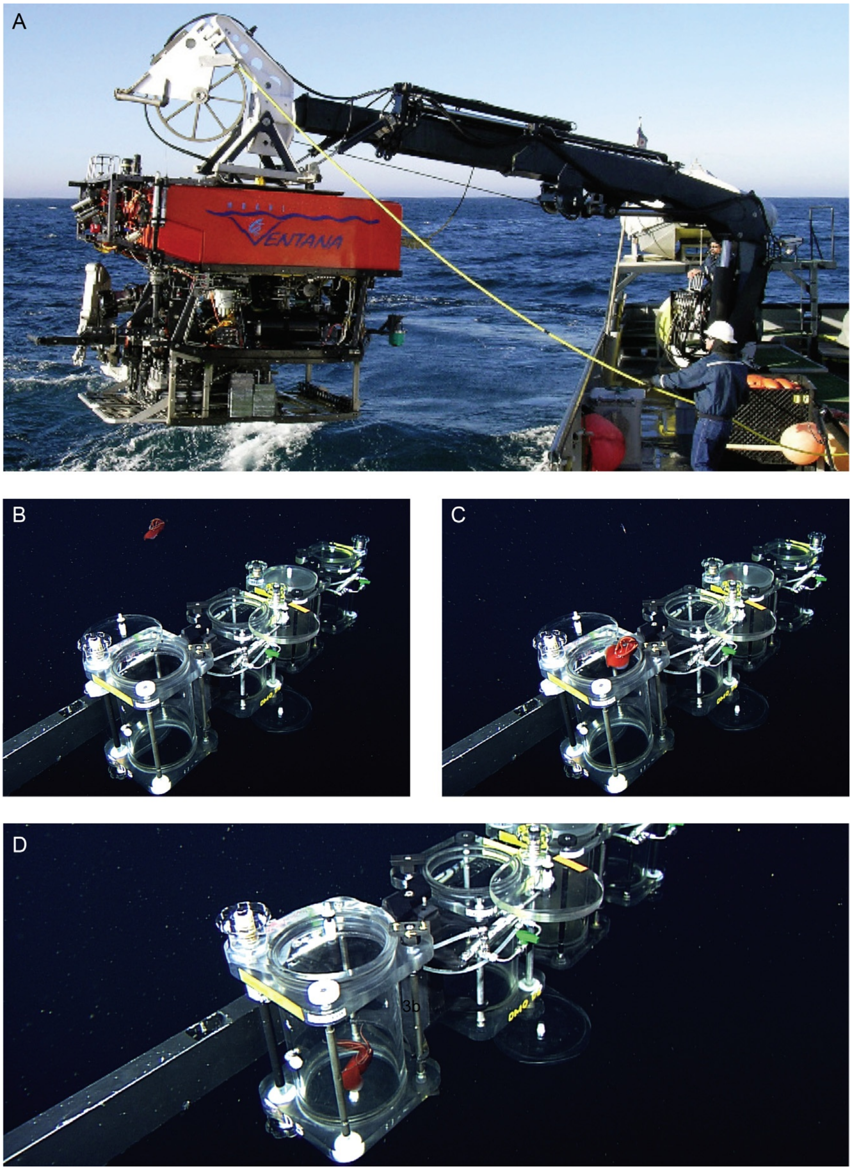

Figure 3.4 (A) The ROV "Ventana" of the Monterey Bay Aquarium Research Institute being deployed in the Monterey Submarine Canyon by R/V *Point Lobos*. (B) *Octopoteuthis deletron* being approached by an opened Detritus sampler (D-sampler) which is mounted on the ROV. (C) The ROV is manoeuvred in such a way that the specimen is positioned over the opened D-sampler. (D) The ROV moves upwards so the specimen is captured inside the D-sampler and the sliding lid of the sampler is closed. A living deep-sea squid is captured. *(A) Photograph Kim Fulton-Bennett © 2004 MBARI. (B–D) © 2013 MBARI.*

et al., 2003). Manned submersibles include those with transparent spheres and those with high-pressure-resistant metal spheres and small portholes. The former allow excellent visibility for the observers—particularly useful for midwater exploration—but have limited depth capability, usually less than 1000 m. The latter, conversely, have much greater depth capability but limited visibility and greater discomfort for the observers.

Unmanned options include remotely operated vehicles (ROVs) (Figure 3.4), which remain connected to the ship by a conducting or fibre-optic cable, allowing control of the vehicle and real-time observations and data, or autonomous underwater vehicles (AUVs), which are pre-programmed for a dive profile prior to release from the ship. Although AUVs have many uses in deep-sea studies, to date they have not been very useful for studying organisms like cephalopods. On the other hand, the ROV has become a standard tool for deep-water biological exploration, resulting in many important cephalopod observations and the collection of excellent specimens (e.g. Robison, 2004). An ROV can remain at depth for prolonged periods, whereas dive duration for manned submersibles is limited by crew endurance and battery capacity. A recent, and expanding, development in ROV operations has been the "telepresence" strategy, in which video, data and two-way communications are linked via satellite between the ship and a shore-based station from which they can be disseminated to scientists and the public at remote command centres (high definition via Internet 2) and any computer connected to the Internet (standard definition via Internet 1). An obvious advantage of this is increased expert participation in the expedition but disadvantages include that specimens generally are not collected and the scientists ashore often cannot dedicate their time to the expedition as intensively as they would if they were aboard. In fact, as this text is being drafted, an ROV is beaming live video ashore from exploration of the Cayman Rise in the Caribbean Sea, including observations of numerous cirrate octopods (http://www.nautiluslive.org).

3.2. Cephalopod collections

Existing institutional collections of cephalopods represent a significant and invaluable resource to the research community. Ranging from small, recent, localized holdings to centuries-old, international repositories, collections contribute to studies in diverse and disparate fields, such as taxonomy, biogeography and reproductive behaviour. In a recent online survey, scientists working in cephalopod research reported accessing specimens from 55 collections around the world (Appendix A). The most commonly accessed were large, well-established collections, such as the US National Museum of Natural History (Smithsonian Institution; Washington, DC, the United States), the Natural History Museum (London, the United Kingdom) and Muséum National d'Histoire Naturelle (Paris, France). However, supplementary material was frequently sourced from smaller institutions as well. In addition, several recent or ongoing collecting programmes were identified around the world, which are equally important as they may help fill gaps in sampling coverage and provide fresh material for studies requiring non-fixed specimens (e.g. genetics). Those programmes open to sampling requests from scientists are given in Appendix B.

3.3. DNA extraction from formalin-fixed tissue

Museum collections hold specimens that are essential to taxonomy. For deep-sea cephalopod species of which very few specimens have ever been caught, museum specimens may be the only possible source of DNA. Unfortunately, most museum specimens are formalin fixed and preserved in ethanol, which makes DNA extraction difficult or impossible (Tang, 2006). Different protocols have been devised for amplifying DNA from museum specimens, such as shown in Fang et al. (2002), who combined gradual dehydration and critical-point drying to successfully amplify high-molecular-weight DNA from formalin-fixed vertebrate tissues. In addition, mitochondrial DNA has been amplified from museum specimens of octopus (Söller et al., 2000) and squid (Carlini et al., 2006). However, there are still many challenges to overcome with formalin-fixed tissue, and failed attempts are generally not reported in the literature (Tang, 2006).

The Barcode of Life Data System (BOLD) is a public compilation of DNA barcodes, which are 652 base pairs from the 5′ end of the mitochondrial cytochrome *c* oxidase subunit I (COI) sequence (Ratnasingham and Hebert, 2007). Strugnell and Lindgren (2007) outlined some considerations and concerns specific to cephalopods in BOLD, such as multiple or nuclear copies of COI, potentially fast rates of evolution, and some uncertainty over whether a single gene is enough to identify species reliably.

Recently, the Barcode Index Number (BIN) system has been introduced, which groups together genetically similar individuals (Ratnasingham and Hebert, 2013). For taxonomy, DNA barcodes can be used to help separate species (Hebert and Gregory, 2005) and have been successful in delineating cephalopod species (Allcock et al., 2011; Dai et al., 2012; Zheng et al., 2012). In addition, DNA barcodes can be used to identify otherwise problematic specimens, such as juveniles (Victor et al., 2009) and badly damaged individuals (St-Onge et al., 2008). Given the great potential for museum material to extend BOLD and the limited success achieved in extracting DNA from formalin-fixed specimens to date (Zhang, 2010), further efforts to improve these techniques should be undertaken, and results reported whether positive or negative.

For example, during a recent review of the Mastigoteuthidae found around New Zealand (Braid, 2013), it became apparent that integrative taxonomy was necessary for working on a group represented mostly by badly damaged specimens, especially as it appears that this family has morphologically similar species with distinct distributions. Therefore, some preliminary tests were conducted on the DNA extraction of formalin-fixed squid tissue using three mitochondrial genes (COI, 16S rRNA and 12S rRNA), trialling combinations of critical-point drying, two DNA extraction protocols and DNA purification, with partial success. Among the most useful protocols were silica-gel column-based extraction, using critical-point-dried tissue combined with a DNA-purification protocol (two sequences recovered out of eight attempted) and alkaline lysis extraction from tissue that had not been critical-point dried (although this only recovered one sequence from 12 samples). Critical-point drying alone was not sufficient to obtain DNA sequences; however, with a DNA-purification step to remove impurities and increase the DNA concentration, some DNA recovery was possible. Overall, it seems that these two steps (critical-point drying of tissue prior to DNA extraction and DNA purification) both assist in sequence recovery from formalin-fixed tissue.

Tissue type may also affect the success of DNA extraction (Tang, 2006), but it appears that DNA extracted from the buccal mass muscle can be successfully amplified (H. Braid, personal observation). The buccal mass is an ideal source of muscle tissue because it is removed during the extraction of beaks for morphological examination. Although DNA extraction is a destructive process, buccal mass tissue can be sampled without damaging important morphological characters. One useful process for providing several different pieces of information and samples is to remove the buccal bulb from specimens prior to fixation, gently extract the beaks (this is usually a simple matter if the specimen has been frozen and then thawed) and store the beaks together with the buccal muscle in 100% ethanol. This ensures that a relatively large piece of muscle tissue is available for molecular work while allowing later confirmation of the parent specimen's identity (should the samples become separated from the whole individual; of course, care should be taken to store subsamples together with parent specimens where possible) by retaining the characteristic beaks together with the tissue.

3.4. Websites, databases and networks

The "Tree of Life" Web Project (ToLweb; http://tolweb.org/), established in 1996, has become one of the leading online repositories of cephalopod information, focussing primarily on systematics, morphology and distribution but also presenting a lot of other biological information. Through the efforts of Richard Young, Michael Vecchione and the late Katharina Mangold (1922–2003), in collaboration with a team of over 20 international researchers, more than 700 pages have been completed for the class Cephalopoda. These remain the most actively updated and informatively complete branches of ToLweb (Maddison et al., 2007). They are particularly useful as taxonomic references, since most taxon pages include images (photos and/or diagrams) and many provide descriptions of key morphological features, as well as general notes on vertical distribution, nomenclature and/or development. In addition to taxonomic information, the ToLweb has many unpublished observations and photographs, in particular for deep-sea cephalopods that are very valuable for biological and ecological studies on these animals. Because of this comprehensive collection of information, which is frequently updated, ToLweb and WoRMS (World Register of Marine Species) (see the succeeding text) were used as the primary references for the current taxonomy of the deep-sea cephalopods discussed herein (Table 3.1).

In addition to web-based resources, advances in ocean science technology have greatly expanded scientific knowledge about the behaviour, ecology and functional morphology of many deep-sea cephalopods; some of this information is also becoming more widely available to the public. The increased feasibility of collecting and analyzing video footage has also necessitated the production and dissemination of field guides to aid in identifying live animals. The Monterey Bay Aquarium Research Institute (MBARI) is a pioneer in this area and maintains a well-established database of deep-sea observations recorded by ROVs during 25 years of operations, a current total of ~19,700 h (S. von Thun, personal communication). From this ROV footage, MBARI's video lab extracts all possible faunal information by annotating the video using their Video Annotation

Reference System (VARS; http://www.mbari.org/vars/). VARS allows biological, geological and experimental observations to be searched for and correlated, together with descriptive and environmental data in the database. This database has revealed unique behaviours of deep-sea cephalopods (e.g. Bush et al., 2009; Hoving and Robison, 2012; Robison et al., 2003), enabled detection of the range expansion of Humboldt squid (*D. gigas*) (Zeidberg and Robison, 2007) and provided unbiased information on distribution and general ecology of deep-sea cephalopods in the Monterey Submarine Canyon (Hunt, 1996). There is a public version of VARS query, and the VARS software is available as an open-source package for use by other institutes. In the northeastern Pacific, *The Marine Life Field Guide iBook* (freely available through the iBook store) has been produced by NEPTUNE Canada (Gervais, 2012) and shows high-quality images of *in situ* observed cephalopod species such as *Graneledone pacifica* Voss and Pearcy, 1990; *Gonatopsis borealis* Sasaki, 1923; and *Dosidicus gigas*. The NEPTUNE Canada cable network gathers live data from instruments deployed and connected on the sea floor off Vancouver Island installed in 800 and 2700 m depth. This tool, installed in area previously lacking an authoritative reference guide, can now be used to help improve the quality of real-time video and photo annotations during cruises and in subsequent studies of archived imagery.

The current ease of communication has facilitated global initiatives and collaborative projects that have increased, or are steadily increasing, our knowledge of deep-sea fauna including cephalopods. For example, following in the footsteps of the Census of Marine Life programme (2000–2010), the INDEEP (International Network for Scientific Investigations of Deep Sea Ecosystems) programme is focusing on determining the global biodiversity and functioning of deep-sea ecosystems. The World Register of Deep-Sea Species (WoRDSS) has recently been launched in collaboration with the WoRMS team (WoRMS Editorial Board, 2014), the Natural History Museum, (London) and the National Oceanographic Centre (Southampton, the United Kingdom) to improve access to deep-sea species information (Higgs et al., 2012). The WoRMS web portal aims to collate the most up-to-date taxonomy with a suite of identification tools (online keys, guides, monographs and papers) recommended by taxonomic experts. Ultimately, it will link directly to a deep-sea field “app” (“Deep Sea ID: A deep-sea field guide”), whose readily available synthesis of information should prove a useful tool for taxonomists, providing a venue for quickly sharing information. It will also be an excellent starting point for people embarking on a studies of new groups or taxa. In linking to an authoritative and updated named database (WoRMS), a consistent taxonomy can also be maintained; WoRDSS will thus be the most up-to-date database of deep-sea taxonomy. Online WoRDSS (http://www.marinespecies.org/deepsea, Glover et al., 2013) lists 419 species of cephalopods as occurring in the deep sea. (The current criterion for inclusion in the WoRDSS database is a sample depth of greater than 500 m, including both pelagic and benthic species; any species recorded below 500 m is included even if it ranges shallower than this depth.)

Although photo imagery is a nondestructive sampling tool for cataloguing the deep sea, identification of species from imagery is often difficult, especially when specimens are not available for confirmation. Organisms can, however, be identified as distinct operational taxonomic units (OTUs) or morphotypes as a basis for future work and detailed species ground truthing through the collection of actual specimens. An ongoing partnership between Ifremer, NOAA, and the University of Plymouth (the United Kingdom) is developing a web-based portal of this kind; initially documenting the Rockall Trough region of the northeast Atlantic, it will soon also include newly collected data from the Bay of Biscay and the western Atlantic (Davies et al., 2012).

3.5. Predators

Large apex predators such as whales, seabirds, seals, sharks and fishes are highly effective samplers, consuming both a great abundance and high diversity of deep-sea cephalopods (Clarke, 1980; Santos et al., 2001; Xavier and Cherel, 2009; Xavier et al., 2003a, 2013). In fact, cephalopods may comprise up to 100% of the total diet in some top predators (Table 3.4), and others are known to feed on more than 35 separate deep-sea cephalopod taxa (e.g. sperm whales; see Gómez-Villota, 2007). Predators are also known to catch larger specimens, and a greater diversity, of cephalopods than are sampled by scientific nets (Clarke, 1977a, 2006; Rodhouse, 1990; Roper, 1974; Staudinger et al., 2014; Wormuth and Roper, 1983; Xavier and Cherel, 2009; Xavier et al., 2006). Furthermore, tracking of cephalopod predators, such as tuna, sharks, seals, sperm whales and seabirds (Block et al., 2011; Croxall et al., 2005; Hindell et al., 2003; Paiva et al., 2010; Phillips et al., 2008; Sims et al., 2008; Xavier et al., 2003b), is currently more feasible than tracking cephalopods directly and is a technique now widely used to support inferences about the vertical and geographical

Table 3.4 Importance of deep-sea cephalopods in the diets of top predators

Top predators	Location	Number of deep-sea cephalopod taxa present in predator's diet	Number of deep-sea cephalopods consumed (%)	Estimated mass of deep-sea cephalopods consumed (%)	Reference
Seabirds					
Wandering albatross *Diomedea exulans*	Subantarctic	>25	93	99	Xavier et al. (2003a)
Grey-headed albatross *Thalassarche chrysostoma*	Subantarctic	>20	100	100	Xavier et al. (2003b)
Black-browed albatross *Thalassarche melanophrys*	Subantarctic	>20	99	99	Xavier et al. (2003b)
Emperor penguin *Aptenodytes forsteri*	Antarctic	>3	100	100	Piatkowski and Pütz (1994)
King penguin *Aptenodytes patagonicus*	Falkland Islands	>9	88	98	Piatkowski et al. (2001)
White-chinned petrel *Procellaria aequinoctialis*	Subantarctic	>5	100	100	Berrow and Croxall (1999)
Whales					
Sperm whale *Physeter macrocephalus*	North Atlantic	>35	100	100	Clarke et al. (1993)
Pygmy sperm whale *Kogia breviceps*	South Pacific	>22	100	100	Beatson (2007)

Continued

Table 3.4 Importance of deep-sea cephalopods in the diets of top predators—cont'd

Top predators	Location	Number of deep-sea cephalopod taxa present in predator's diet	Number of deep-sea cephalopods consumed (%)	Estimated mass of deep-sea cephalopods consumed (%)	Reference
Pilot whale *Globicephala melaena*	South Pacific	>5	70	74	Clarke and Goodall (1994)
Bottlenose whale *Hyperoodon planifrons*	South Pacific	>20	100	100	Clarke and Goodall (1994)
Seals					
Southern elephant seal *Mirounga leonina*	Antarctic	>5	98	98	Daneri et al. (2000)
Southern elephant seal *Mirounga leonina*	Subantarctic	>10	99	99	Rodhouse et al. (1992)
Weddell seal *Leptonychotes weddellii*	Antarctic	>5	65	74	Clarke and MacLeod (1982)
Fishes					
Patagonian toothfish *Dissostichus eleginoides*	Subantarctic	>10	75	98	Xavier et al. (2002)
Conger eel *Conger conger*	North Atlantic Ocean	>1	7	8	Xavier et al. (2010)
Porbeagle shark *Lamna nasus*	South Indian Ocean	>15	100	100	Cherel and Duhamel (2004)

Sleeper shark *Somniosus* cf. *microcephalus*	South Indian Ocean	>15	100	100	Cherel and Duhamel (2004)
Lantern shark *Etmopterus* cf. *granulosus*	South Indian Ocean	>3	100	100	Cherel and Duhamel (2004)
Longnose lancetfish *Alepisaurus ferox*	Central Indian Ocean	>10	85	95	Potier et al. (2007)
	Northwest Pacific Ocean	>15	81	90	Okutani and Kubota (1976)

The number of deep-sea cephalopods consumed (%) and estimated mass (%) corresponds to the deep-sea cephalopods consumed within the cephalopod component in the diets of predators.

distribution of cephalopods and about predator–cephalopod interactions that cannot be obtained by other means (Davis et al., 2007; Ropert-Coudert et al., 2006; Staudinger and Juanes, 2010; Wilson et al., 2002). Thus, dietary data from teuthophagous predators can be used to make inferences on the biology and ecology of deep-sea cephalopods.

Various methods can provide data on the cephalopod component of predator diets (Barrett et al., 2007; Karnovsky et al., 2012; Xavier et al., 2005), including direct observations (e.g. observing an albatross feeding at the sea surface) and the examination of the stomach contents of dead animals and from scats/faeces. Traditionally, the examination of stomach contents has been one of the most widely used methods for studying the diets of predators, having the advantage of potential quantification of prey importance (e.g. the contribution of cephalopod species by frequency of occurrence, by number and by mass) at the time of sampling. Some cephalopod predators are more suitable samplers than others. The longnose lancetfish, *Alepisaurus ferox* Lowe, 1883, for instance, forages on mesopelagic cephalopods. Its stomach contents are extremely useful for biological studies as food is stored in the stomach and digestion takes place in the intestine; relatively intact prey items can therefore be recovered from the stomach (Okutani and Kubota, 1976; Potier et al., 2007). In other instances where less-intact stomach contents are recovered, the original body sizes of digested cephalopods can often be estimated from measurements of their beaks, which are more resistant to digestion than soft tissues and often accumulate in the stomachs of predators (Clarke, 1962, 1986; Lu and Ickeringill, 2002; Xavier and Cherel, 2009). However, beaks can be retained in predator stomachs for 9 months or longer (Xavier et al., 2005); therefore, caution must be used to differentiate among fresh (i.e. with transparent parts or with flesh attached) and highly eroded beaks, to ensure accurate interpretation of the results (Xavier and Cherel, 2009; Xavier et al., 2011). Prey digestion rates also vary widely depending on the size of the predator and of the prey; these variable rates can considerably affect the results obtained from stomach contents for soft-bodied or small prey (e.g. cephalopods, fishes or crustaceans) that can be digested completely. For example, some fishes can be completely digested within 12 h in petrels, seals and penguins, but digestion rates differ according to the fish species consumed (Helm, 1984; Hilton et al., 1998; Jackson and Ryan, 1986; Wilson et al., 1985). The same may be true for different cephalopod species.

Several recent biochemical methods have provided additional novel ways to gain further information about deep-sea cephalopods collected from predator stomachs. Trace elements can be used to determine geographical distribution and to differentiate stocks (e.g. Arbuckle and Wormuth, 2014); stable isotopes of carbon and nitrogen (from fresh cephalopod tissue or tissue recovered from predators) act as ecological tracers of habitat use and trophic level (Cherel and Hobson, 2005); DNA barcoding and fatty-acid analysis can be used to identify cephalopods to species and indicate consumed prey taxa (Braid et al., 2012; Dai et al., 2012; Hoving and Robison, 2012); and chemical pollutants shed light on the accumulation and transfer of persistent anthropogenic pollution through remote deep-ocean communities up to charismatic and endangered megafauna (Unger et al., 2008). In addition, these techniques can help reconstruct seasonal, annual and decadal shifts in oceanographic conditions over varying spatial scales through the analysis of biogenic structures such as beaks or gladii that reflect varying time periods of nutrition and habitat use (e.g. Barrett et al., 2007; Cherel and Hobson, 2005; Karnovsky et al., 2012; Ramos and Gonzalez-Solis, 2012).

4. SYSTEMATICS, DIVERSITY, BIOGEOGRAPHY AND EVOLUTION OF DEEP-SEA CEPHALOPODS

4.1. Evolutionary pathways to modern deep-sea life: Implications from the cephalopod fossil record

In contrast to numerous shallow-water deposits of epicontinental seas, examples of deep-sea deposits and hence records of deep-sea fossil communities are extremely rare; the few fossil deep-sea faunal assemblages known to date have yielded no cephalopods. However, inferences of evolutionary pathways leading to modern deep-sea cephalopods can be made from indirect evidence, including the palaeoenvironment in which fossil cephalopods have been found and/or their functional morphology. By far, the greatest source of fossil cephalopod information is the preserved buoyant shell (phragmocone), which would have imposed a physical habitat depth limit as it does in modern cephalopods such as *Nautilus*, *Spirula* and *Sepia* (Figure 3.5). However, thanks to sedimentary deposits known to exhibit extraordinary soft tissue preservation (called *Konservat-Lagerstätten*, literally "conservation preservation sites"), a relatively good understanding of external and internal morphology can also be gleaned, particularly for coleoids.

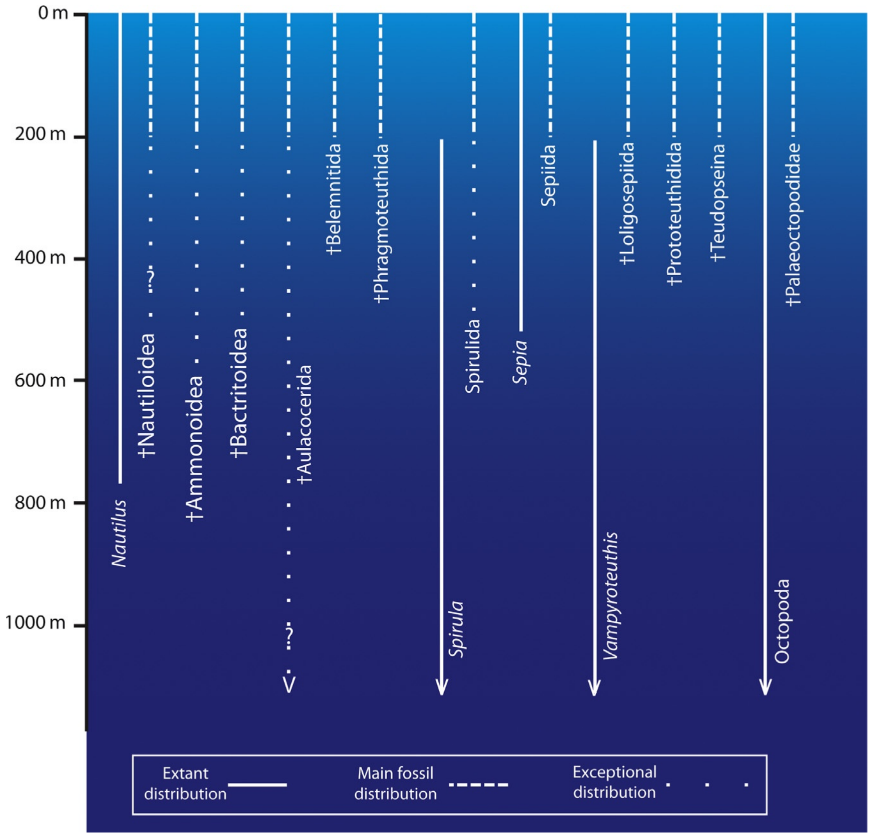

Figure 3.5 Depth distributions of fossil cephalopods (mainly inferred from functional morphologies).

4.1.1 Nautiloidea and Ammonoidea

The large majority of fossil ectocochleate (external shelled) cephalopods were restricted to epicontinental shelf and slope habitats. They first appeared during the Cambrian period (about 500 million years ago) as bottom-associated monoplacophoran-like molluscs (Kröger et al., 2011), and their distributions at any time were determined by transgressions (sea-level rise) and regressions (sea-level decrease). According to depth-range estimates based on shell-strength calculations, only a few of these taxa could dive as deeply as modern *Nautilus* (Daniel et al., 1997; Hewitt and Westermann, 1988; Hewitt et al., 1989; Westermann, 1973); there is no positive evidence from the fossil record that early ectocochleates were adapted to permanent life in the deep sea.

4.1.2 *Coleoidea*

As with ectocochleates, the fossil record of endocochleate coleoids is confined to shallow inland and shelf areas. Coleoids most likely originated during the Late Devonian or in early Carboniferous times from bactritoid ancestors. Bactritoidea was an extinct group of ectocochleate cephalopods with a straight (orthoconic) phragmocone; this lineage also gave rise to the Ammonoidea. Bactritoids are considered to have been inhabitants of epi- to upper mesopelagic water depths (Westermann, 1973).

4.1.2.1 Belemnoidea

Based on their palaeobiogeographic distribution, belemnoids (Aulacocerida, Phragmoteuthida, Belemnitida and Diplobelida) are generally considered to have been neritic, similar to the recent loliginids (Doyle, 1990; Jeletzky, 1966; Westermann, 1973). Several exceptions may have occurred within the Aulacocerida, where some taxa are known from oceanic deposits (e.g. Triassic of Timor, Indonesia). Westermann (1973) believed that these forms were capable of withstanding higher hydrostatic pressures (maximum estimated implosion depth 1000 m).

4.1.2.2 Decapodiformes

Early predecessors of the recent Decapodiformes probably evolved during the Late Jurassic or Early Cretaceous period from belemnoid diplobelids (Fuchs et al., 2012, 2013; Kröger et al., 2011). These early decapods (either stem-lineage representatives or already within the spirulid lineage), commonly called groenlandibelids, have been found in neritic sediments but most probably drifted there postmortem from oceanic provinces. Therefore, it has been suggested that groenlandibelids—similar to present-day *Spirula*—inhabited mesopelagic waters above the continental slopes (Fuchs et al., 2013; Hewitt et al., 1991).

However, the direct ancestors of mesopelagic *Spirula*, commonly called "Tertiary spirulids," have been found in epicontinental deposits, and the shell morphologies of Eocene–Miocene *Beloptera* and *Spirulirostra* suggest a demersal lifestyle (Young et al., 1998). This indicates that *Spirula* migrated downwards into meso- to bathypelagic waters only 5–10 million years ago. Fuchs (2012) recently concluded that, over the course of evolution, the spirulid shell has progressively retained more early ontogenetic shell characters. These neotenous traits suggest a highly derived (rather than a primitive) morphology and lifestyle for *Spirula*.

Early representatives of the Sepiida (*Ceratisepia*) first appeared in the Late Cretaceous and generally co-occurred with spirulids in Cenozoic neritic deposits (e.g. Eocene *Belosepia*). Since only a handful of modern sepiid species can live in waters deeper than 400 m (Sherrard, 2000), it appears that the bulk of these taxa have retained their approximate original depth distribution.

While spirulids and sepiids are primarily shallow-water inhabitants, Arkhipkin et al. (2012) recently hypothesized that teuthoid squids may have originated in the deep sea. According to this scenario, the squid gladius derived from a belemnitid shell through "...reduction of the dysfunctional rostrum-phragmocone system with subsequent decalcification..." as a physiological adaptation of a life in oxygen-poor deep-water habitats. If this is true, then neritic provinces (e.g. those inhabited by modern loliginid squids) might have been secondarily invaded, unless loliginids are cuttlefishes that have lost the phragmocone rather than oegopsids that moved into shallow waters (Young et al., 1998).

4.1.2.3 Octopodiformes

Octopodiformes (*Vampyroteuthis*, Cirrata, Octopoda) most probably derived from a belemnoid subgroup, the Phragmoteuthida (Jeletzky, 1966). This Middle Triassic divergence must have happened—as in squids—through decalcification of the inner shell and the development of a gladius, which is well known throughout the entire Mesozoic (e.g. Fuchs, 2006; Fuchs and Larson, 2011a,b; Fuchs and Weis, 2008, 2010; Fuchs et al., 2007a,b). In contrast to meso- to bathypelagic *Vampyroteuthis*, these gladius-bearing octopodiforms occupied nektonic or nektobenthic niches in shallow waters; the *Vampyroteuthis* lineage must thus have retreated from shallow waters at some point. However, *Vampyroteuthis* has conserved many ancestral morphological characters.

The Octopoda, comprising Cirrata (Cirroctopoda) and Incirrata, stem from a subgroup of gladius-bearing octopodiforms called Teudopseina (Bizikov, 2004; Fuchs, 2009; Fuchs and Larson, 2011a; Fuchs and Weis, 2010; Fuchs et al., 2009; Haas, 2002). Although still unknown, the hypothetical last common ancestor of the Octopoda (cirrates and incirrates) must have appeared very similar to living cirroctopods. Whereas ancestral cirrates have not been identified with certainty in the fossil record (perhaps the earliest true cirrate was already a deep-sea dweller?), our knowledge about the earliest members of the Incirrata is comparatively good. The first unambiguous octopods with a clearly bipartite gladius vestige appear in Late

Cretaceous epicontinental deposits, indicating moderate water depths (Fuchs et al., 2009); these palaeoctopods already lacked cirri but still possessed fins. In the light of recently proposed phylogenies (e.g. Lindgren et al., 2012; Strugnell et al., 2004, 2009), it appears plausible to assume multiple deep-sea colonizations for various octopod subgroups (Voss, 1988).

In conclusion, expansion into the deep sea from shallow origins is a common and independent occurrence observable in almost all cephalopod subgroups; teuthoid squids, however, may have first arisen and radiated in the deep sea and only later colonized shallow waters.

4.1.3 Misconceptions regarding "living fossils"

The term "living fossil" can only be used with accuracy for *Vampyroteuthis*, since it differs little from its Mesozoic shallow-water-dwelling ancestors. The use of this term for *Nautilus* is still premature, since information about the soft-part morphology of its ancestors remains scarce (e.g. number of arms? number of gills?). Certainly, the *Nautilus* shell exhibits a general conservatism, but in detail (e.g. shape of the conch, course of sutures and position of the siphuncle), it differs significantly from its latest known ancestors, such as *Eutrephoceras* and *Cenoceras* (see Ward, 1984). *Spirula* is definitely not a "living fossil" and must rather be considered as a highly derived cephalopod.

4.2. Diversity and Systematics

Few cephalopod species that spend the majority of their adulthood in the deep sea are well understood, even those considered abundant. New genera are regularly described, and many families are known to contain unnamed species and species complexes. It is perhaps surprising that, in a class with just ~850 extant nominal species (Table 3.1), such systematic uncertainty should remain.

4.2.1 Information sources for deep-sea cephalopod biodiversity

While physical collections form an indispensable resource (as discussed in Section 3.2), their material can only represent a small cross-section of the deep-sea cephalopod fauna. Many of the taxa represented in institution holdings are at the smaller end of the size range for this class and often have soft, gelatinous bodies. Most trawled specimens, after being tumbled in nets with more robust-bodied animals, reach the surface in poor condition, severely limiting their potential for morphological examination. This has resulted in some difficulties in species delineation, with many early species descriptions based only on single and/or badly damaged specimen(s).

A good example is the 21 nominal species of *Architeuthis* that have been described since the first description by Steenstrup in 1857. Genetic data have recently shown that *Architeuthis* comprises a single cosmopolitan species, *A. dux* (Winkelmann et al., 2013), with ~20 synonyms. (Winkelmann et al., 2013). Many deep-sea taxa remain poorly represented in collections because of the relative infrequency of deep sea collecting expeditions, and for some groups (e.g. large species of *Onykia*, *Mesonychoteuthis* and *Architeuthis*), accidental collection as by-catch in commercial fisheries targeting other species remains the main source of available material.

The condition of this material varies greatly, and the geographical distributions of these taxa may appear artificially narrow based on localized commercial fishing effort. Retention (and later, fixation and storage) of this material can pose additional challenges due to its lack of economic value (to fisheries), as well as spatial constraints and the volume of hazardous chemicals required, especially for large specimens.

For some species, extensive museum collections can provide insight into intraspecific variations in morphology, but for many taxa, holdings are restricted to a few individuals. In addition, different life stages and states of maturity for a species might not be represented comprehensively by specimens in collections. However, examination of whole (or partial) physical specimens is no longer the sole means of gaining insight into deep-sea cephalopod diversity. With the recent advances in underwater imagery, and the greater human presence in the deep sea, species are increasingly identified within their natural habitat in their natural (i.e. unpreserved) form. In fact, some species, such as a large magnapinnid known from the Pacific (Vecchione et al., 2001), remain known exclusively from video footage; no physical specimen has ever been positively identified in collections.

4.3. Biogeography

Fries (2010) created a distribution map using primary literature and databases (OBIS and AquaMaps) (Figure 3.6) to illustrate the worldwide distribution of scientific records of the Cephalopoda, including both coastal and deep-sea habitats. It highlighted obvious gaps in cephalopod studies, namely, the Arctic, southwest Atlantic, Indian and Pacific Ocean. A brief summary of studies that have focused specifically on the deep sea (below 200 m) in the major ocean basins follows. They are far from the only studies conducted but are a broad indication of the information available for each region.

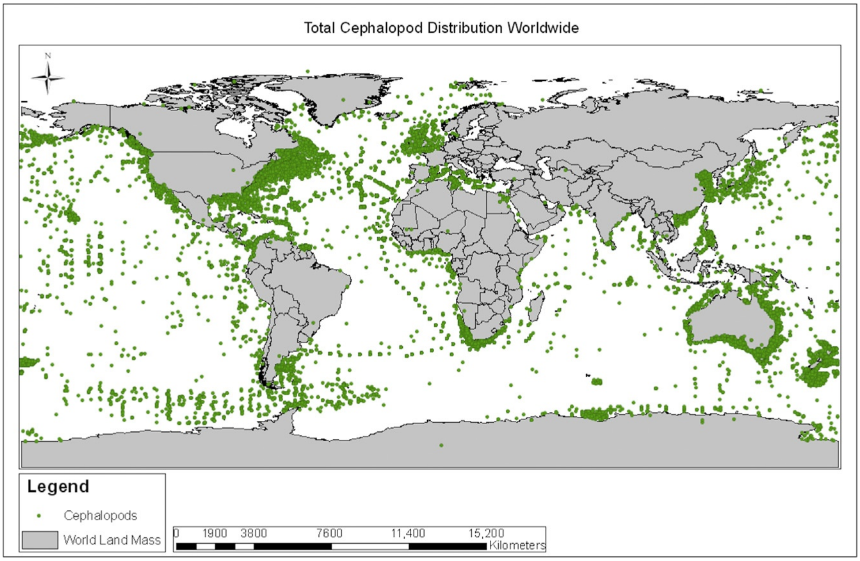

Figure 3.6 Global cephalopod distribution based on meta-analysis study demonstrating worldwide cephalopod distribution and regional gaps requiring future study. *With permission from Fries (2010).*

4.3.1 Atlantic Ocean

Several overviews of the deep-sea fauna have been published, as well as a number of regional reviews. For example, large-scale depth-related diversity patterns of cephalopods in the Atlantic were examined in the open-ocean and deep-sea regions by Rosa et al. (2008) through extensive literature review. Cephalopod diversity was found to peak along continental shelves and within the epipelagic zone and to decline with depth below 200 m. This contrasts with patterns observed for other macrofauna as well as for other molluscan groups such as gastropods and bivalves (Rex et al., 2005). In the southwestern Atlantic, Haimovici and Perez (1991) and Haimovici et al. (2009) have inventoried the deep-sea cephalopod fauna of the Brazilian slope down to 600 m; Guerra et al. (2001) also reported 21 species off the Patagonian Shelf down to 1500 m and showed that benthic octopods penetrate this area within the plume of cold sub-Antarctic waters and are pushed northwards into the South Atlantic by the Falkland/Malvinas current. Future studies were suggested on either side of this plume to investigate the presence of cold water-adapted species. In the northern Atlantic, midwater cephalopods were examined off Nova Scotia during the years 1986–1989 by Vecchione and Pohle (2002), who found 63 species from

28 families, in depths between 169 and 4800 m. Subsequent investigations under the MAR-ECO initiative reported 56 species from along the northern Mid-Atlantic Ridge (Vecchione et al., 2010b) and 50 cephalopod species from the southern portion of the ridge (Perez et al., 2012). In the northeastern Atlantic, cephalopods have been documented from the surface to the sea floor at great depths, including an impressive record of a deep-sea *Muusoctopus* species observed feeding on baitfall (porpoise) at a depth of 2555 m (Kemp et al., 2006). Collins et al. (2001) reviewed the distributions of deep-water (150–4850 m) benthic and benthopelagic cephalopods in this region and identified 36 species of cephalopods from 14 families. Judkins (2009) also reported 129 cephalopod species to inhabit the wider Caribbean, which includes the Gulf of Mexico, Caribbean Sea and a portion of the central western Atlantic. In her study, abundance, distribution and diversity differences were analysed and distribution maps were created for each species, with deep-sea taxa accounting for 45% (58 species) of species documented.

4.3.2 Pacific Ocean

In the southeastern Pacific, a distribution and diversity study conducted off the coast of Chile revealed 71 oceanic species, with the majority found below 200 m (Ibañez et al., 2009). In the northeastern Pacific Ocean, Sinclair and Stabeno (2002) recorded 11 deep-sea cephalopod species from the southeastern Bering Sea, and a field guide to squids and octopodiforms of the eastern North Pacific and Bering Sea was completed in 2009 (Jorgensen, 2009). A deep-sea octopod, *Graneledone* cf. *boreopacifica*, has also been collected near an active hydrothermal vent at 1459 m (Voight, 2000). Given the difficulty of sampling adult cephalopods, cephalopod larvae can also be used to investigate the systematics, distribution and abundances of epiplanktonic squid larvae, such as a study conducted in the California Current (Okutani and McGowan, 1969). Other paralarval studies in the Pacific have focused on the diverse Gonatidae (Hunt and Seibel, 2000; Kubodera and Jefferts, 1984a,b), as well as the ommastrephids (Harman and Young, 1985). A comprehensive study on epipelagic cephalopods was undertaken by Okutani (1974). Young (1972b) also documented 30 species of pelagic deep-sea cephalopods from southern Californian waters, more than a dozen of which have also been observed by MBARI's ROV programme. These cephalopods include *Vampyroteuthis infernalis*, histioteuthids, enoploteuthids, gonatids, cranchiids, octopoteuthids, onychoteuthids and members of the chiroteuthid families (e.g. Bush et al., 2007, 2009; Hoving et al., 2013b;

Hunt, 1996; Robison et al., 2003). In the mid-Pacific, while surveying the Cross Seamount in the mid-Pacific Ocean for mesopelagic micronekton, 22 species of cephalopod were recorded (De Forest and Drazen, 2009). Notable recent findings in the western Pacific along the coast of Japan, both from cruise material and live *in situ* observations category, include those of Kubodera and Mori (2005, for *Architeuthis*), Kubodera et al. (2007, for *Taningia*) and a collaborative expedition yielding the first-ever video footage of a live *Architeuthis dux* at depth (600–900 m, Widder, 2013).

4.3.3 Indian Ocean

Cephalopod captures in the deep Indian Ocean have been scarce, or poorly reported, until recently; specimens were previously only known to be collected as part of other research projects like the International Indian Ocean Expedition in the 1960s. However, at least some regions and environments appear to have quite high species diversity: Nesis (1986) reported 50 species of cephalopods from four tropical Indo-West Pacific-type seamounts, and work conducted by Piatkowski (1991) in the Arabian Sea examined the distribution of pelagic cephalopods to 1000 m. Laptikhovsky et al. (submitted) also recorded at least 68 cephalopod species, from 26 families, from along the Southwest Indian Ridge.

4.3.4 Polar Oceans

Kubodera and Okutani (1994) identified 44 eledonine octopods in the Southern Ocean, describing the distribution and systematics of the group. Allcock et al. (2001) studied octopods in the eastern Weddell Sea to a depth of 1000 m and found eight species of incirrate octopods, three of which were undescribed, and many other subsequent species descriptions have originated from the region (Allcock et al., 2004; Vecchione et al., 2005, 2009b). Xavier et al. (1999) compiled data obtained between 1886 and 1997 in the Southern Ocean and found that 21 species of oegopsid squids had been reported from depths below 200 m. The geographical distributions of each were documented with respect to bathymetry, ocean fronts and sea-ice extent. However, large areas remain from which no data have been reported. Additional studies on cephalopods, using predators as samplers (e.g. Xavier et al., 2006, on albatrosses), have also been conducted in this region, giving further insight into cephalopod distribution and abundance. In the Arctic Ocean, Nesis (2001) discussed the distributional ranges of seven cephalopod species inhabiting the region, concluding that they represented a mixture of circumpolar and non-circumpolar distributions. Another study focusing on distribution and predation was conducted for 36 cephalopod species by Gardiner and Dick (2010) based on past records including museum collections, government reports, international and national databases, published articles and personal communications. Distribution maps were created for each; however, no records could be found for some areas, so coverage of the entire region remained incomplete. Most recently, Golikov et al. (2013) provided new data on the distribution of three Arctic cephalopod species (*Todaropsis eblanae* Ball, 1841; *Todarodes sagittatus* Lamarck, 1798; *Teuthowenia megalops* Prosch, 1849; and *Gonatus fabricii* Lichtenstein, 1818) and showed significant range extensions for these deep-sea cephalopods.

4.4. Combined approaches to cephalopod systematics

Cephalopod taxonomy has advanced markedly in the last few decades. This is partly due to improved exploratory technology and increased sampling but has also resulted from the application of molecular techniques, which provide additional suites of traits that can be used to define species and examine their phylogenetic relationships. While molecular techniques have been utilized primarily in shallower-water taxa to date, due to the relative availability of fresh tissue, they are also increasingly being used as a tool to study deep-sea forms. Although species are traditionally identified by morphology, this approach can underestimate the "true" number of species if cryptic species are present. Similarly, DNA-sequencing techniques can over- or underestimate the "true" number of species when inappropriate markers are used. Thus, a cautionary approach should be taken in determining species boundaries by including as many suites of character traits as possible, ideally both morphological and molecular, and incorporating combined analyses of multiple genetic sequences from each individual (covering both nuclear and mitochondrial DNA sequences).

To distinguish genetically among different species in sympatry, it is essential to independently confirm any phylogenetic hypothesis based on molecular data by either morphological or unlinked molecular characters (Feulner et al., 2007; Milinkovitch et al., 2002). Frankham et al. (2012) have identified approximately 26 definitions of species and, depending upon which concept is followed, different numbers of species and disparate groupings result. These researchers demonstrated that the definition and determination of species have financial, legal, biological and conservation implications and gave an insightful review of this subject.

Recently, considerable advances in our understanding of the higher-level systematics of coleoid cephalopods have occurred. Morphological studies have proven useful in classifying species within subfamilies and genera but less so in determining higher-level relationships due to problems involving the determination of character independence, apomorphic loss of characters or assessment of homology/homoplasy (Young and Vecchione, 1996). This is particularly important for deep-sea cephalopods, where most of the family-level diversity within the class is found. High rates of evolution in cephalopods, coupled with their radiation into numerous habitats, have confounded our ability to recover consistent phylogenetic relationships using both morphological and molecular data (Lindgren et al., 2012).

Historically, molecular studies have produced conflicting results, perhaps due to limited taxon or gene sampling. Strugnell and Nishiguchi (2007) attributed the lack of clear resolution to the different alignment and analysis combinations that have been used in studies of cephalopod phylogenetics. Consistent among these results, however, is the monophyly of the Octopoda, Argonautidae, Oegopsida and Ommastrephidae based on two sequence homology methods and three analysis methods, with the Bathyteuthidae the sister taxon of the Oegopsida in each case. The paper by Strugnell and Nishiguchi (2007) also gave a useful summary of the outcomes of various molecular analyses to 2007 and advocated the use of a variety of different alignment and analysis strategies in phylogenetic analysis.

Lindgren et al. (2012) generated the most comprehensive multigene phylogeny to date, based on 10 genes for over 400 cephalopod taxa (representing 42 of 47 families). In addition to providing a well-supported phylogeny, these researchers created a character matrix of habitat type and morphological characters from which to infer ancestral character states and test for correlation between habitat and morphology to study the phylogenetic and environmental forces driving character evolution. Convergent evolution was shown for all six morphological characters analysed, three of which (autogenic photophores, cornea and accessory nidamental glands) correlate with habitat and therefore environmental pressures. This study also serves to underline the importance of a combined approach in formulating robust phylogenetic hypotheses. Their results confirmed monophyly for almost all major orders and families studied except the Octopodidae *sensu lato*, which is a highly divergent group morphologically, with numerous species complexes (Norman and Hochberg, 2005; Strugnell et al., 2013).

In addition to providing insight into the phylogenetic relationships among higher-level cephalopod groups, genetic data can be used to improve natural history knowledge of individual species. For species that appear endemic to relatively small geographical areas (e.g. *Watasenia scintillans* Berry, 1911), molecular data can provide insight into population dynamics and gene flow. For others that appear to have global distributions, like the currently monospecific *Taningia*, *Vampyroteuthis* and *Spirula* (or the rarely encountered but apparently cosmopolitan *Asperoteuthis acanthoderma* Lu, 1997; see Judkins et al., 2009), genetics may reveal systematic complexities not immediately evident from morphological data alone. The genus *Taningia*, for example, has been considered monospecific for more than 150 years but may in fact have at least two species (J. Kelly, personal observation). In contrast, *Architeuthis*, a genus with 21 named species (of which recent authors have generally accepted between one and four, e.g. Jereb and Roper, 2010), now appears to contain a single cosmopolitan species, according to mitochondrial genomic work by Winkelmann et al. (2013). Moreover, the level of nucleotide diversity in *A. dux* is extremely low, suggesting a possible recent bottleneck or expansion from one region into the remainder of the temperate oceans.

4.5. Future priorities in cephalopod systematics

Despite our enhanced knowledge of deep-sea cephalopods due to recent technological advances, our ability to collect and identify cephalopods in some areas remains limited. Many developing countries lack the financial support and technology necessary for deep-sea research, which results in gaps in knowledge for particular regions. Similarly, data coverage in remote regions is limited due to logistical and financial constraints (McIntyre, 2009). In general, areas requiring the most attention are currently the southeast Pacific, southwest Atlantic, and the Indian and Arctic Oceans.

Targeting taxa that are in particular need of focused taxonomic research effort is difficult because, while the deep ocean is largely underexplored in general (Webb et al., 2010), some families are well known from some geographical regions and poorly known from others for a variety of reasons. Globally, collection and exploration efforts have been concentrated in particular areas—not necessarily areas of greatest importance or need, but largely as a result of disparate funding and resource opportunities. Furthermore, most cephalopod studies in the deep sea result from funded projects aimed at other questions/problems. For example, deep-sea benthic octopods have received some focused research effort in polar regions and Australasia but are poorly known elsewhere, although recent work in the southeastern Pacific based on specimens obtained off the shelf and slope of Chile (Ibañez et al., 2012) is now filling another knowledge gap.

Some groups, however, have notoriously unstable systematics worldwide. Foremost among them are the squid families Cranchiidae, although Voss (1980) substantially stabilized the genera, and Chiroteuthidae, which is suspected to contain several unconfirmed new genera, as well as several undescribed species in the existing genera *Chiroteuthis* and *Asperoteuthis* (Young and Roper, 2011a). One of the least-studied families appears to be the Brachioteuthidae; within *Brachioteuthis*, several species have been named but only partially described, and additional new species have been recognized (ToLweb, 2012); consequently, all named brachioteuthid taxa are in need of review and disambiguation. The validity of all taxa is now under review. Mastigoteuthids are similarly problematic, although the New Zealand fauna has recently been reviewed by Braid (2013). Octopoteuthids are similarly poorly understood and are under current review by P. Jereb, A. Guerra and J. Kelly. Families such as Cranchiidae, Opisthoteuthidae and Mastigoteuthidae, known to have high local diversity in some regions (the latter being the most abundant cephalopods in the deep sea) (M. Vecchione, personal observation), should be particular candidates for revision as such patterns suggest that additional new species may be present. Research directions can also be guided by the availability of existing preserved specimens in museum collections or the potential to obtain fresh material from active collecting programmes. Wherever possible, morphological and molecular techniques should be used together in future taxonomic revisions, with resulting sequences submitted to GenBank and BOLD and distribution records to OBIS.

5. LIFE CYCLES OF DEEP-SEA CEPHALOPODS

5.1. Reproduction

5.1.1 General reproductive system morphology

All cephalopods are dioecious (i.e. the sexes are separate). The male reproductive system is divided into an unpaired testis; a vas deferens; a spermatophoric (or spermatophore-producing) organ; a spermatophoric (or Needham's) sac, where spermatophores are stored; and a terminal organ (or "penis"), a prolongation of the spermatophoric sac. The terminal organ may have an extensor capacity and is involved in spermatophore transfer in some deep-sea cephalopods; alternatively, one or more of the male arms may bear structural and glandular modifications related to spermatophore transfer (e.g. Hoving, 2008; Nesis, 1995). Although the majority of male cephalopods bear only the left gonoduct, some deep-sea species exhibit paired (and functional) gonoducts (*Selenoteuthis scintillans* Voss, 1958, *Lycoteuthis* spp. and *Stigmatoteuthis* spp.) (Nesis, 1987a, 1995; Voss et al., 1998).

The female reproductive system is divided into an ovary, one or two oviducts and one or two oviducal glands. Paired oviducts and oviducal glands occur in Vampyromorpha, incirrate octopods and in most Oegopsida, with the oegopsid family Pyroteuthidae being an exception: *Pterygioteuthis* spp. possess only the right gonoduct, and *Pyroteuthis* spp. may bear a reduced right gonoduct. In sepiids, sepiolids, myopsids and cirrate octopods, only the left gonoduct is present. With few exceptions (i.e. Enoploteuthidae), all decapods bear a pair of nidamental glands in the anterior ventral region of the mantle cavity. All decapods except oegopsids also bear an additional pair of glands called "accessory" nidamental glands, which house symbiotic bacteria that are passed to the egg capsules (Barbieri et al., 2001). Although the exact process is largely unknown, all glands (oviducal, nidamental and accessory nidamental) are involved in egg-capsule formation, except in incirrate octopods, in which the oviducal glands form the cement material used by the female to attach eggs on the substrate (Froesch and Marthy, 1975).

5.1.2 Spermatophores

Coleoid spermatophores are considered to be one of the most elaborate reproductive structures in the animal kingdom (Mann, 1984). With the exception of cirrate octopods, which produce an unusual spermatophore (or "sperm packet"; Villanueva, 1992), coleoid spermatophores generally consist of a sperm mass, a cement body and an ejaculatory apparatus, being enveloped by the outer and middle tunics (Figure 3.7; Marian, 2012a,b). From the outside to the median axis of the spermatophore, the ejaculatory apparatus tube consists of the inner tunic, the middle and inner membranes and the spiral filament (Figure 3.7), the latter bearing minute stellate particles (Marian, 2012a,b). Hess (1987) provided an extensive overview of the spermatophores of a wide variety of cephalopods, including deep-sea species. Spermatophore sizes (relative and absolute) vary considerably among deep-sea coleoids, ranging from absolute lengths of a few millimetres in *Abralia* spp. to 20 cm in the giant squids (Hoving et al., 2004). *Heteroteuthis*

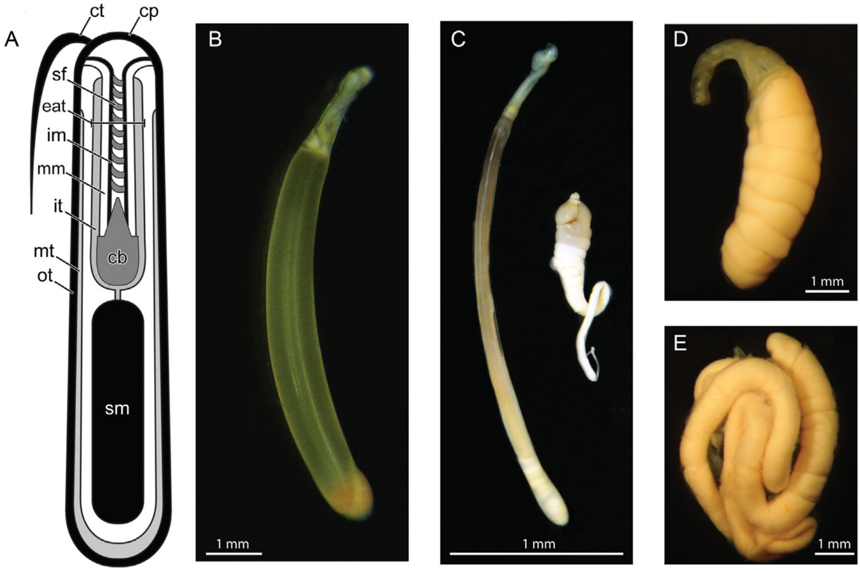

Figure 3.7 Deep-sea cephalopod spermatophores and spermatangia. (A) Diagrammatic representation of a generalized squid spermatophore. (B) *Histioteuthis miranda* spermatophore. (C) *Discoteuthis discus* spermatophore (left) and spermatangium (right). (D) and (E) *Heteroteuthis dispar* spermatophore (D) and spermatangium (E). Abbreviations: cb, cement body; cp, cap; ct, cap thread; eat, ejaculatory apparatus tube; it, inner tunic; im, inner membrane; mm, middle membrane; mt, middle tunic; ot, outer tunic; sf, spiral filament; sm, sperm mass. *(A) Originally published in Marian et al. (2012) and reproduced with kind permission from Springer Science and Business Media. (B) Originally published in Hoving et al. (2010a) and reproduced with permission. (D) and (E) Originally published in Hoving et al. (2008b) and reproduced with kind permission from Springer Science and Business Media.*

dispar (Rüppell, 1844) may have the proportionally largest spermatophores among deep-sea cephalopods (SpL = 33–43% ML; Hoving et al., 2008b). A general schematic diagram of a coleoid spermatophore is provided in Figure 3.7.

Spermatophores' intricacy is not only structural: when properly triggered, coleoid spermatophores are able to function autonomously in a process called the "spermatophoric reaction" (e.g. Hoving and Laptikhovsky, 2007; Hoving et al., 2009; Mann, 1984; Marian, 2012a,b). The spermatophoric reaction is an osmotically controlled process that comprises the evagination of the spermatophoric tunics and membranes, leading to the extrusion of the cement body and to the formation of the spermatangium (everted spermatophore containing the sperm mass). Mated females often bear spermatangia attached to their bodies in a variety of (sometimes taxon-specific) locations.

The number of spermatophores stored in the spermatophoric sac may vary widely in deep-sea squid, from approximately 80 in *Ancistrocheirus lesueurii* Orbigny, 1842 (Hoving et al., 2006), to about 250 in *Lycoteuthis lorigera* Steenstrup, 1875 (Hoving et al., 2007); 1000 in *Octopoteuthis sicula* Rüppell, 1844 (Hoving et al., 2008a); and 100–1800 in ommastrephids (e.g. Nigmatullin et al., 2003). Spermatophorogenesis (spermatophore formation) has been intensively studied in ommastrephid squids, including its ontogenetic aspects (e.g. Nigmatullin et al., 2003). These authors demonstrated that there is a distinction between physiological and functional maturity in male squid, with the production of "tentative" (devoid of sperm) and "false" spermatophores (spermatophores with very small sperm volume) during submaturity. These are constantly released through the terminal organ until the mature stage is reached and fully functional spermatophores are produced, at which point output can be considerable: a daily production rate of 10–20 spermatophores was estimated for mature males of the ommastrephid *Illex argentinus* (Arkhipkin and Laptikhovsky, 1994).

Spermatophore production apparently begins relatively early, and somatic growth continues after the production of the first spermatophores, and spermatophores may be stored in the spermatophoric sac for ca. 4.5 months (Hoving et al., 2010a). This strategy was postulated to be associated with the deep-sea environment: where encounters between mates are rare, the chances of fertilization could be maximized by beginning spermatophorogenesis earlier in the life cycle (Hoving et al., 2010a). Although this may be true, spermatophore production in coastal and epipelagic species also starts early in life and is associated with somatic growth (e.g. Nigmatullin et al., 2003).

The sperm mass of the spermatophore may contain millions of spermatozoa (Mann, 1984). Detailed ultrastructural data on the spermatozoa of one deep-sea decapod (*Rossia pacifica* Berry, 1911, Fields and Thompson, 1976) and six deep-sea octopodiform species (*Opisthoteuthis persephone* Berry, 1918, and Healy, 1993; *Graneledone gonzalezi* Guerra, Gonzalez and Cherel, 2000, and Roura et al., 2009; *Bathypolypus bairdii* Verrill, 1873 and *B. sponsalis* P. Fischer and H. Fischer, 1892, Roura et al., 2010a; *Vulcanoctopus hydrothermalis* Gonzalez and Guerra in González et al., 1998; Roura et al., 2010b; and *Vampyroteuthis infernalis* Healy, 1989, 1990) are currently available in the literature and suggest that some sperm characters may be useful for gaining insight into the systematics and phylogenetics of cephalopods, across all taxonomic levels.

Much remains to be investigated regarding sperm and spermatophore morphology in deep-sea cephalopods. In addition to contributing to the systematics and phylogenetics of the class as a whole (Hess, 1987), such detailed morphological data (such as those available for neritic squid; Marian and Domaneschi, 2012) can provide hints to sperm-transfer mechanisms (Marian, 2014).

5.1.3 Mating behaviour

Mating in deep-sea cephalopods has long been a matter of conjecture. Mating observations have been rare (e.g. Roper and Vecchione, 1996), and behaviour has often been inferred from characteristics of preserved specimens (e.g. Hoving, 2008; Nesis, 1995). As will be discussed, however, recent evidence gathered from on-board analysis of freshly caught individuals, as well as from observations performed through submersibles, has substantially improved our knowledge of the copulatory behaviour of deep-sea cephalopods. Nevertheless, much remains to be discovered, and the morphological analysis of museum specimens, particularly when combined with observations of living individuals, remains a powerful tool in providing insights into this elusive aspect of deep-sea cephalopod biology.

Spermatophores are transferred to female cephalopods by two main methods: with the aid of the hectocotylus (a male arm apparently modified specifically for spermatophore transfer) or directly through the terminal organ. Where present, the hectocotylus generally bears structural and/or histological specializations (such as the absence or modification of sucker rings and/or the presence of papillae, lobes or glandular pads, to name a few; Nesis, 1995) that differentiate it from other arms. Most of these specializations are believed to be directly involved with spermatophore transfer, that is, to facilitate holding and manipulating spermatophores. In incirrate octopods, the hectocotylus is one member of the third arm pair (Norman and Sweeney, 1997), while in decapods, one or both of the ventral arms are modified (Nesis, 1995), except in sepiolids, cranchiids and histioteuthids, in which one or both of the dorsal arms are modified (Hoving et al., 2008b; Voss, 1980; Voss et al., 1998). Spermatophore transfer through the hectocotylus appears to be the sole strategy utilized by neritic cephalopods and is also utilized by some groups of deep-sea species, such as sepiolids (Hoving et al., 2008b), incirrate octopods (Voight, 1997) and some oegopsid squids (e.g. Ommastrephidae, Enoploteuthidae, Ancistrocheiridae, Lycoteuthidae, Pyroteuthidae, Thysanoteuthidae and Cranchiidae; Nesis, 1995), including some oegopsids that reproduce in true deep-sea strata (e.g. some Cranchiidae; Nesis, 1995). This strategy is generally inferred from the presence of a hectocotylus in preserved specimens, but oceanic species from the family Ommastrephidae have also been observed to transfer spermatophores presumably by the hectocotylus: *Dosidicus gigas* (Gilly et al., 2006; Nigmatullin et al., 2001), *Todarodes pacificus* (Okutani, 1983) and *Sthenoteuthis* spp. (Zuyev et al., 2002). In these cases, the mating position was "head to head," and the spermatophores were deposited on the buccal membrane, where these species bear seminal receptacles (see "Spermatangium attachment sites"). A possible observation of mating in a deep-sea incirrate octopod *Vulcanoctopus hydrothermalis* was also reported by Rocha et al. (2002), in which four males were apparently mating with the same female simultaneously, three of them "mounting" the female and one male mating "at distance" by stretching its hectocotylus (a common strategy within shallow-water incirrate octopods). A copulatory behaviour between two males of separate deep-sea octopod genera had also previously been documented by Lutz and Voight (1994), at a depth of 2500 m along the crest of the East Pacific Rise. The authors postulated that this strategy could be related to the fact that in the deep sea, mate encounters are rare. Recently, Hoving et al. (2012) found evidence that indicate (intraspecific) same-sex sexual behaviour for the deep-sea squid *Octopoteuthis deletron* Young, 1972. In a number of males observed by ROV, implanted spermatangia could be discerned in similar body locations as those often seen on females, and such "mated" males were encountered approximately as frequently as females.

At present, the exact process of spermatophore transfer via hectocotylus in deep-sea cephalopods can only be inferred from observations of neritic species. For example, based on what is known for loliginid squids (e.g. Drew, 1919; Hanlon and Messenger, 1996), neritic sepiolids (e.g. Rodrigues et al., 2009) and idiosepiids (Sato et al., 2013), males of most deep-sea oegopsid squids and sepiolids probably retrieve a group of spermatophores from the terminal organ during mating with the aid of the hectocotylus, which then transfers them to the site of attachment on the female body. For deep-sea benthic incirrate octopods, the process of spermatophore transfer might be similar to what has been observed in shallow-water species (e.g. Wodinsky, 2008): the spermatophore is placed into the spermatophoric groove (on the hectocotylized arm) by the terminal organ; the spermatophore then travels along by peristalsis to the arm tip, which inserts the spermatophore into the distal oviduct of the female. In some pelagic incirrate octopods such as *Argonauta*, *Tremoctopus* and *Ocythoe*, dwarf males possess a very elaborate hectocotylus, which remains enclosed in a protective sac until mating (Naef, 1921–1923). During copulation, the hectocotylus presumably everts from this sac, retrieves the spermatophore, autotomizes itself and relocates to inside the mantle cavity or even the reproductive system of the female (Naef, 1921–1923).

The other type of spermatophore transfer, that is, directly through the terminal organ, appears restricted to deep-sea cephalopods (e.g. Architeuthidae, Gonatidae, Octopoteuthidae, Onychoteuthidae and Pholidoteuthidae). This mode of transfer was long postulated from the presence, in several deep-sea species, of a long terminal organ (Figure 3.8) combined with the absence of a hectocotylus. In these cases, the terminal organ has recurrently been found (in preserved specimens) with its tip protruding and sometimes considerably extending beyond the mantle margin (e.g. Bolstad, 2006; Jackson and Jackson, 2004, Figure 3.8). This mode of transfer has recently been confirmed by two complementing papers. Based on a moribund specimen of *Onykia ingens* (Smith, 1881) (Onychoteuthidae), Arkhipkin and Laptikhovsky (2010) demonstrated that the terminal organ has the capacity to extend itself to almost the same length as the whole body of the animal. Then, Hoving and Vecchione (2012) made the first observations of copulation in a deep-sea squid (*Pholidoteuthis adami* Voss, 1956) by ROV, wherein the terminal organ extended considerably from the mantle cavity through the funnel to reach the female body, while the male arms (not hectocotylized) played no role beyond holding the female (Figure 3.8). In both mating pairs observed by Hoving and Vecchione (2012), the male was parallel to and positioned above the female but oriented in the opposite direction (posterior mantle above the female's head) and "upside down" (ventral side up) (Figure 3.8; ROV observations). Extending through the funnel, the terminal organ reached the dorsal surface of the female's mantle, at approximately the level of the fin insertions (Figure 3.8). This region has been observed in museum specimens as a common site of spermatangium attachment (Hoving and Vecchione, 2012).

Previously, presumed mating in *Brachioteuthis beanii* had been observed by a submersible, although alternative hypotheses (e.g. cannibalism) could also explain the observed parings (Roper and Vecchione, 1996). In this case, mating was in a "head-to-tail" position, with the presumed male grasping the posterior portion of the presumed female's mantle. Judging from the observations from Hoving and Vecchione (2012) on *P. adami*, the

Figure 3.8 Spermatophore transfer through the terminal organ. (A) Mating in *Pholidoteuthis adami* documented by ROV. Specimen size approximately 680 mm ML. This behaviour was observed during an expedition by NOAA's Ocean Exploration programme. (B) Mature male of *P. adami* from a museum collection, showing the terminal organ extending through the funnel. *(A) and (B) originally published in Hoving and Vecchione (2012) and reproduced with permission.*

presumed male could be transferring spermatophores to the female at the region of the ovary, but contrary evidence from Young (1978) and K. Bolstad (personal observation) has found spermatangia in the buccal membrane of *Brachioteuthis*.

Pholidoteuthis adami was one of the species in which spermatophore transfer was previously hypothesized to be performed by the terminal organ, based on preserved specimens observed with the terminal organ tip extending beyond the mantle margin and lacking a hectocotylus (Nesis, 1995). Following confirmation of this hypothesis, as discussed in the previous paragraph, other deep-sea squid families with similar reproductive structure morphologies (e.g. Octopoteuthidae, Onychoteuthidae, Gonatidae and Architeuthidae; Nesis, 1995) are anticipated to perform spermatophore transfer through the terminal organ as well. Several questions remain to be answered, however. For example, the mechanism enabling terminal organ extension is completely unknown. Detailed morphological investigation could help reveal whether the terminal organ of deep-sea squid function, for instance, as muscular hydrostats. Spermatophore orientation and placement are poorly understood even for species with a hectocotylus. In the case of the terminal-organ-mediated transfer, however, the mechanism by which the spermatophores are correctly oriented remains unknown yet must have great importance as they are always released with the aboral ends first (the oral end of the spermatophore being the implanting region). In some species, the tip of the terminal organ exhibits complex morphology (e.g. Nesis, 1995), suggesting a possible role in spermatophore orientation and placement, but much remains to be discovered about this enigmatic process.

5.1.4 Spermatangium attachment sites

Spermatangium attachment sites vary considerably among deep-sea cephalopods. In some species, no special receptacles are present, and the spermatangia are implanted into external surfaces of the female's body, such as the mantle, arms, tentacles and head region (e.g. Architeuthidae Hoving et al., 2004; Cranchiidae Nesis et al., 1998; Cycloteuthidae Clarke, 1980; Histioteuthidae Voss et al., 1998; Octopoteuthidae Hoving et al., 2008a, 2010b; Onychoteuthidae Bolstad and Hoving, 2011; Pholidoteuthidae Hoving and Vecchione, 2012; and Sepiolidae Hoving et al., 2008b; Figure 3.9), and/or within the mantle cavity in the vicinity of the genital opening (e.g. Cranchiidae Nesis et al., 1998; Enoploteuthidae Burgess, 1998; Histioteuthidae Voss et al., 1998; *Illex* spp. O'Dor, 1983; Onychoteuthidae Laptikhovsky et al., 2007; and Sepiolidae Hoving et al., 2008b).

In other species, specialized receptacles for spermatangium deposition/implantation are present, such as those found in the nuchal region of squids

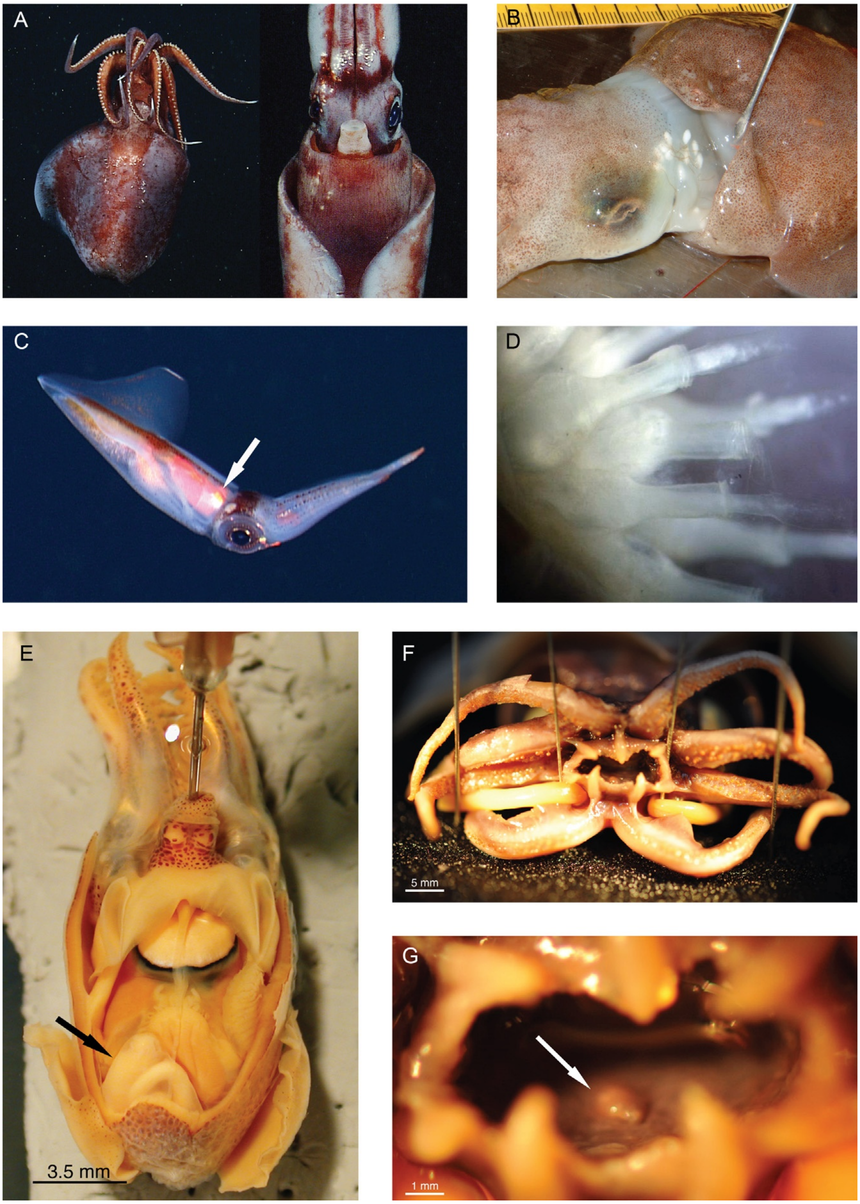

Figure 3.9 Spermatangium attachment sites. (A) and (B) Spermatangia implanted on external surfaces of the female body in (A) *Octopoteuthis deletron* (ML ca. 130 mm) and (B) *Rossia macrosoma*. (C) *Abraliopsis felis*, which has spermatangium receptacles in the nuchal region (arrow). (D) Spermatangia attached to the nuchal receptacle of *A. felis*. (E) Posterior seminal sac (arrow) containing a spermatangium in *Heteroteuthis dispar*. (F) and (G) Seminal receptacle (arrow) in the ventral buccal membrane of *Bathyteuthis berryi*. *(A) © 2006 MBARI. (B) Originally published in Hoving et al. (2009); (C) © 2010 MBARI; (E) originally published in Hoving et al. (2008b) With kind permission from Springer Science and Business Media; (F) and (G) originally published in Bush et al. (2012). All reproduced with permission.*

of the enoploteuthid families (Ancistrocheiridae, Enoploteuthidae, Lycoteuthidae and Pyroteuthidae; Burgess, 1998; Hoving et al., 2007; Hoving and Lipinski, 2014; Young and Harman, 1998; Figure 3.9). Some species of Rossinae (Sepiolidae) bear a bursa copulatrix (which involves the modification of the distal oviduct) or a ridged area near the oviduct (Hoving et al., 2008b), where spermatangia are found; in the pelagic Heteroteuthinae (Sepiolidae), a posterior seminal sac accommodates typically a single large spermatangium (Hoving et al., 2008b; Figure 3.9). Female vampire squid (*Vampyroteuthis infernalis*) bear large subcutaneous pouches located in front of the eyes, each able to store a spermatangium (Pickford, 1946, 1949). Other groups bear seminal receptacles, specialized sperm storage organs with morphological and histological specializations that enable them to store spermatozoa released from the spermatangia (Marian, 2014). For example, in some ommastrephids, numerous seminal receptacles occur in a ring on the buccal membrane (Arkhipkin et al., 1998; Ikeda et al., 1993; Nigmatullin and Markaida, 2009; Nigmatullin et al., 2002; Zuyev et al., 2002), and in bathyteuthids, a single main receptacle is located ventrally on the buccal membrane (similar to the neritic loliginids and sepiids; Bush et al., 2012; Figure 3.9). Exceptions to this general pattern (the presence of sperm and/or spermatangium receptacles) include some species in which the spermatangia are implanted within the mantle cavity in the vicinity of the genital opening (e.g. *Illex* spp. O'Dor, 1983; some Enoploteuthidae Burgess, 1998).

In incirrate octopods, seminal receptacles, when present, are located inside the oviducal glands (Froesch and Marthy, 1975). Octopods from incirrate *Eledone*, however, lack spermathecae in the oviducal glands and store spermatozoa inside the ovary, where the apical filaments of the oocytes serve as sperm storage sites (Perez et al., 1990). The sperm packets of cirrate octopods are transferred to the female oviducal gland (Aldred et al., 1983), but the presence of a seminal receptacle in this group is uncertain.

Basically, there are three types of spermatangium attachment in coleoids (Marian, 2014). One of them is typical of incirrate octopods, where the spermatangium is "plugged" into the distal oviduct, finding its way through it into the oviducal gland or into the ovary (Froesch and Marthy, 1975; Mann et al., 1970; Perez et al., 1990; Wells and Wells, 1972; Figure 3.10). Decapods may exhibit "shallow attachment," in which only the base of the spermatangium is implanted and cemented into the female tissue (e.g. Ommastrephidae, Durward et al., 1980; Sepiidae,

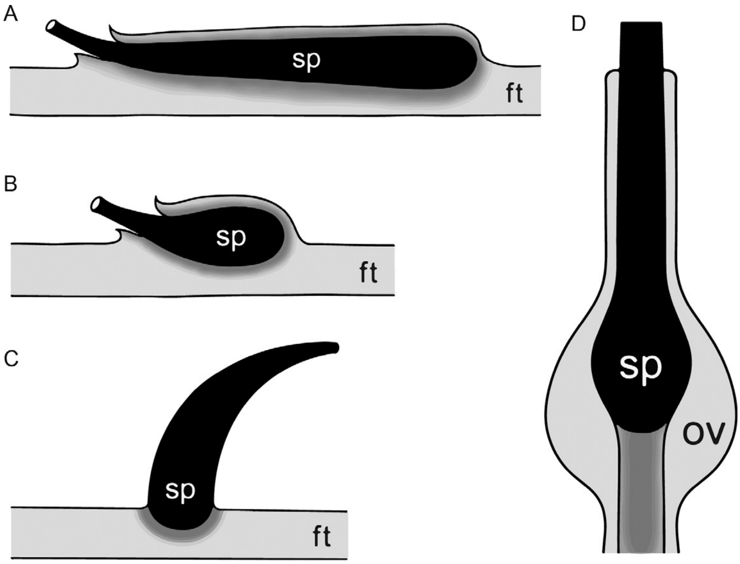

Figure 3.10 Types of spermatophore attachment in cephalopods. (A–B) Deep implantation (e.g. Architeuthidae, Cranchiidae and Octopoteuthidae). (C) Shallow implantation (e.g. Ommastrephidae, Enoploteuthidae). (D) Plugged attachment (e.g. incirrate octopods). Abbreviations: ft, female tissue; ov, oviducal gland; sp, spermatangium. *Originally published in Marian (2014) and reproduced with permission from Taylor & Francis Ltd. www.tandfonline.com.*

Hanlon et al., 1999; Figure 3.10), or "deep implantation," in which nearly the entire length of the spermatangium is implanted into female tissue (e.g. Architeuthidae Hoving et al., 2004; Cranchiidae Nesis et al., 1998; Octopoteuthidae Hoving et al., 2008a; and Sepiolidae Hoving et al., 2009; Figure 3.10). Shallow attachment is found in both neritic (e.g. Loliginidae) and deep-sea squids (e.g. Enoploteuthidae), but deep implantation appears restricted to deep-sea squid.

Until recently, the mechanism that enables deep implantation of spermatangia has been uncertain. Early hypotheses attributed the enabling of spermatangium implantation to extrinsic factors, such as a hydraulic system presumably performed by the terminal organ, or cuts made by the male hooks or beaks (Jackson and Jackson, 2004; Nesis et al., 1998; Norman and Lu, 1997). However, several recent lines of evidence (Hoving and Laptikhovsky, 2007; Hoving et al., 2009) have demonstrated that deep implantation is autonomous, that is, achieved by the spermatophore itself. Based on experimental data from neritic squid and published information from deep-sea squid, a common mechanism was proposed to explain both shallow and deep implantation (Marian, 2011, 2012a,b), involving the action of the ejaculatory apparatus and its containing spiral filament and stellate particles. This theoretical model, however, still needs to be tested (Marian, 2012b).

It is relevant to note that, among such variation in sperm-transfer mechanisms, some common patterns have been identified. Marian (2014) found evidence for convergent evolution in some cephalopod reproductive strategies: shallow implantation and seminal or spermatangium receptacles may have coevolved more than once independently (including in deep-sea lineages) and deep-spermatangium implantation multiple times independently, depending on the phylogenetic hypothesis under consideration. Arkhipkin and Laptikhovsky (2010) hypothesized that the evolution of sperm-transfer mechanisms in Decapodiformes followed two distinct pathways: transfer of spermatophores by the hectocotylus to specialized female receptacles in several neritic and epi/mesopelagic squids and transfer of spermatophores through the terminal organ with deep implantation of spermatangia on the surface of the female's body in several deep-water squids. However, this hypothesis has not yet been successfully tested. Also, because exceptions to this suggested pattern exist (e.g. bathypelagic squids having seminal receptacles, Bush et al., 2012), it remains unclear whether and how the evolution of these reproductive strategies has been influenced by the marine habitat. Further investigation requires detailed morphological and functional data on the reproductive system of the majority of the species (not currently available) and further resolution of the conflicting phylogenetic hypotheses among cephalopods (Marian, 2014).

5.1.5 Fertilization and egg (mass) production

Despite the great abundance of some oceanic cephalopods, the egg masses of many remain very poorly known or entirely unknown. Ommastrephids produce large, spherical, neutrally buoyant pelagic egg masses, which have been reported for several species (Bower and Sakurai, 1996; Durward et al., 1980; Laptikhovsky and Murzov, 1990; O'Shea et al., 2004; Staaf et al., 2008). These egg masses are spawned "on" the pycnocline (the layer between water masses of different densities) where the density gradient is the steepest, and are subsequently generally found in relatively shallow waters (up to 30 m). Encounters with egg masses are infrequent, however, and even for the well-studied, commercially valuable species *Dosidicus gigas*, of egg masses have rarely been reported (Staaf et al., 2008). Egg masses of *Thysanoteuthis rhombus* Troschel, 1857, have been repeatedly described in the literature (e.g. Guerra et al., 2002; Nigmatullin and Arkhipkin, 1998; Nigmatullin et al., 1995), and recently, pelagic egg masses encountered in South African waters were attributed to a *Lycoteuthis* species (Roberts et al., 2011).

In some deep-sea cephalopod families, females maintain contact with their eggs and embryos after spawning, a phenomenon known as post-spawning egg care or "brooding" (Okutani et al., 1995; Seibel et al., 2005). Brooding is common in benthic and pelagic octopods including deep-sea species (e.g. Voight and Grehan, 2000; Young, 1972a, 1995, 2013) but has also been reported in two deep-sea squid families: Gonatidae and Bathyteuthidae (Arkhipkin and Bjørke, 1999; Bower et al., 2012; Bush et al., 2012; Okutani et al., 1995; Seibel et al., 2000, 2005).

Fertilization mechanisms in deep-sea cephalopods remain a similar matter of conjecture and extrapolation. The species for which information on fertilization does exist all spawn in shallow oceanic waters in the upper 100 m, but summarizing the available information for these species is the only way to infer how fertilization and spawning may happen in species that spawn in the deep sea. Observations by Durward et al. (1980) and O'Dor and Balch (1985) on *Illex illecebrosus* (Lesueur, 1821) have suggested the following scenario. Thousands of eggs are released into a concentrated gel secreted from the nidamental glands. The gel is mixed with sperm from the attached spermatangia and possibly whole spermatangia that break loose from the mantle wall. The whole mixture (gel, eggs and sperm) is moved into the funnel and combined with a large quantity of water by mantle contractions (O'Dor and Balch, 1985). The occurrence of empty spermatangia inside the egg masses of *Illex illecebrosus* suggests that fertilization may also happen inside the egg mass (Durward et al., 1980).

One clue in understanding the fertilization processes in other cephalopods is the location of stored sperm. Presumably, eggs are passed along this location, wherever it may be in various taxa, so that sperm can be brought into contact with the eggs. In most ommastrephids (except *Illex*), as well as in most gonatids, sperm is stored on the buccal membrane, either in spermatangia that are superficially implanted (Gonatidae; H.J. Hoving, personal observation) or inside seminal receptacles (Ommastrephidae; e.g. Ikeda et al., 1993; Nesis, 1995). Eggs leaving the funnel are presumably subsequently brought into contact with the sperm from the buccal area. *Thysanoteuthis rhombus* is another species that stores sperm in spermatangia on the buccal membrane, but its characteristic cylindrical egg masses suggest a somewhat different process of spawning and fertilization. One proposed fertilization scenario for this species is as follows: (1) A mass of nidamental-gland secretions is moulded into a cylinder (Nigmatullin et al., 1995); (2) eggs from the oviduct are coated by jelly from the oviducal gland, forming threads that merge into one in the mantle cavity; (3) this single thread with two series of eggs is passed close to the buccal area, perhaps during exit via the funnel, and is fertilized; (4) the thread, with now-fertilized eggs, is wrapped around the cylinder of nidamental-gland secretion, forming the final columnar egg mass (e.g. Nigmatullin et al., 1995).

Species with post-spawning egg care (i.e. gonatids and bathyteuthids) also store sperm on the buccal membrane, but in these taxa, fertilization mechanisms remain unknown.

Enoploteuthids lack nidamental glands; their eggs are coated in clear oviducal-gland secretions and released as thin threads (Hayashi, 1989; Young and Harman, 1985; Young et al., 1985). These presumably pass along both sides of the nuchal cartilage, where spermatangia are stored in spermatophore receptacles (Burgess, 1998; Nesis, 1995). The collection of individual enoploteuthid eggs in plankton samples may indicate one of three things: eggs are spawned individually (Laptikhovsky, 1999); the jelly holding the eggs together in threads disintegrates after contact with water (Nesis, 1995); or the egg threads are damaged by plankton nets, releasing individual eggs (R. Young, personal communication). In other squids where females have been found with spermatangia stored in the nuchal area (*Ancistrocheirus lesueurii* Hoving and Lipinski, 2014; *Taningia danae* Hoving et al., 2010b; *Lycoteuthis lorigera* Hoving et al., 2007; and Pyroteuthidae Lindgren et al., 2013), eggs are also presumably passed along this region before fertilization, and spawning mechanisms might be similar to those of the Enoploteuthidae.

From these hypothesized scenarios, it seems that in decapod cephalopods in general, fertilization of the eggs occurs outside the body (external fertilization). However, as the eggs and sperm are first brought together in a confined space inside the mantle, nuchal area or arms, fertilization might more properly be considered "confined external" (Hanlon and Messenger, 1996; Naud and Havenhand, 2006). True internal fertilization has been hypothesized for the sepiolid *Heteroteuthis dispar* because the anatomy of this species allows for eggs to be fertilized inside the oviduct or ovary (Rüppell, 1844)—the posterior seminal receptacle in *H. dispar* is in contact with the visceropericardial coelom (Hoving et al., 2008b). Internal fertilization also happens in incirrate octopods, in which sperm is stored within the oviducal gland or within the ovary (Froesch and Marthy, 1975; Perez et al., 1990), and possibly also in the deep-sea squid *Planctoteuthis oligobessa* Young, 1972, where spermatangia have been found inside the ovary around the oocytes (Hoving, 2008; Young, 1972b). For species where sperm (or spermatangia) are implanted on external body sites, far from the oviduct openings, fertilization methods can only be hypothesized (Hoving, 2008). In *Octopoteuthis* spp., spermatangia have been reported all over the outer surface of the female's body, including the anterior and posterior mantle, (both dorsally and ventrally), on the head, on the arms and on the fins and tail (Hoving et al., 2008a, 2012; Nesis, 1995). In these species, immobile stored sperm from spermatangia may be mobilized by a chemical cue (e.g. from secretions from the nidamental or oviducal glands) produced by egg spawning. This cue could trigger the movement of the sperm from the implanted spermatangia through the water to the eggs, as has been suggested for other species (Durward et al., 1980).

5.1.6 Reproductive strategies

Coleoid cephalopods are considered semelparous (Boyle and Rodhouse, 2005; Cole, 1954): the spawning of eggs happens during one reproductive cycle, although eggs may be spawned over an extended period of time. Within semelparity, different traits (e.g. variability in egg size, ovulation and spawning patterns and patterns of somatic and reproductive growth) define the exact reproductive strategy that a cephalopod species uses. Based on the differences between these traits, it is possible to further categorize cephalopod reproductive strategies even if the overall strategy is semelparity (Hoving, 2008; Laptikhovsky et al., 2007; Rocha et al., 2001). It should be noted that recent observations on the first known mature female of *Kondakovia longimana* Filippova, 1972, have also suggested the potential for multiple reproductive cycles and, therefore, iteroparity in this species (Laptikhovsky et al., 2013). However, evidence remains inconclusive.

Various categories of reproductive strategies were recognized for some cephalopod families (e.g. Nesis, 1995; Nigmatullin and Laptikhovsky, 1994) before the comprehensive classification by Rocha et al. (2001) was published; this study defined five reproductive strategies for cephalopods based on ovulation patterns and whether or not growth occurred between spawning events. Four of these strategies can be found in coleoid cephalopods: (1) continuous spawning (as occurs in cirrate octopods), (2) simultaneous terminal spawning (spawning all eggs at once), (3) multiple spawning (eggs spawned progressively in separate batches, with growth between spawning events), and (4) intermittent terminal spawning (similar to multiple spawning, but without growth between spawning events). The classification proposed by Rocha et al. (2001) mostly applied to neritic species, because little information was available at that time on deep-sea cephalopods other than cirrates. Using new data on the deep-sea squids *Gonatus antarcticus* Lönnberg, 1898, and *Onykia ingens*, Laptikhovsky et al. (2007) divided coleoid cephalopods into two groups based on their ovulation patterns: species that ovulate (and spawn) their eggs synchronously ("simultaneous terminal spawners" sensu Rocha et al., 2001) and species that ovulate asynchronously (and spawn repeatedly). Asynchronous ovulation may involve the asynchronous ripening of individual eggs or batches of eggs. Repeated spawning includes the strategies "multiple spawning" and "intermittent terminal spawning" as defined by Rocha et al. (2001). Sample size in studies on deep-sea squids is generally small and often does not allow for identification of growth in between spawning events, making "multiple spawning" a challenging strategy to identify. However, using the division proposed by Laptikhovsky et al. (2007), it is possible to allocate squid species to a reproductive strategy based on oocyte length frequencies.

Repeated spawning is known to occur in various pelagic deep-sea cephalopods including members of the Enoploteuthidae, Lycoteuthidae, Ommastrephidae, Pyroteuthidae and Thysanoteuthidae (e.g. Hoving, 2008; Laptikhovsky et al., 2007); this strategy is also likely to occur in other species with asynchronous ovulation (e.g. Octopoteuthidae and Architeuthidae). Squids with this strategy have relatively high fecundities and release their small eggs in pelagic egg masses (strings, spheres or cylinders) in very high numbers. For example, 35,000–75,000 eggs have been estimated in egg masses of *Thysanoteuthis rhombus* (Nigmatullin et al., 1995), up to ~100,000 in *Illex illecebrosus* (Durward et al., 1980) and 200,000 in *Todarodes pacificus* (Bower and Sakurai, 1996). Based on the number of eggs observed in the oviduct, *Lycoteuthis lorigera* likely produces egg masses of 1000–3000 eggs (Hoving et al., 2014). Sepiolids also commonly have asynchronous ovary maturation, high fecundity and continuous repeated spawning, a suite of reproductive strategies that may have contributed to their evolutionary success in deep-sea habitats (Laptikhovsky et al., 2008). Moreover, benthic deep-sea sepiolids have considerably larger egg sizes (>10% ML) than shallow-water relatives (Laptikhovsky et al., 2008). Pelagic sepiolids (Heteroteuthinae) produce small eggs, have relatively high fecundity (Hoving et al., 2008b) and are thought to attach eggs to the sea floor (Okutani and Tsuchida, 2005).

Pelagic incirrates display the most elaborate reproductive strategies within cephalopods (Naef, 1921–1923; Young and Vecchione, 2008): females of *Argonauta* spp. secrete a delicate, calcareous, shell-like structure in which they brood multiple batches of eggs; females of *Tremoctopus* spp. brood multiple batches of eggs attached to elongated rods, which are held by suckers at the bases of their dorsal arms; *Ocythoe tuberculata* Rafinesque, 1814, is ovoviviparous, with the eggs developing in the oviducts until hatching. In some cirrate octopods, egg laying is apparently continuous throughout most of the lifespan, as has been suggested for *Opisthoteuthis* spp., based on observations that continuous egg production occurs in the ovary, growth continues after the onset of maturity and oviducal-gland fullness is not related to body size (Boyle and Daly, 2002; Villanueva, 1992). Moreover, females of these species are often found with a single mature egg in the distal region of the oviduct; this egg, ready to be spawned (most probably individually), is encapsulated in a sticky substance secreted by the oviducal gland that becomes a rigid shell when exposed to sea water (Vecchione et al., 1998b). Although Aldred et al. (1983) found sperm packets inside the oviducal gland of *Cirrothauma murrayi* Chun, 1911, subsequent surveys of the oviducal gland of several specimens of *Opisthoteuthis* failed to find stored sperm (Boyle and Daly, 2002), which would be expected in a continuous-spawning strategy in the deep sea. *Vampyroteuthis infernalis* apparently releases individual eggs in midwater (Nesis, 1995; Pickford, 1946, 1949).

Cephalopods with synchronous ovulation ("simultaneous terminal spawning" *sensu* Rocha et al., 2001) accumulate ripe ova in the ovary and presumably spawn all their eggs at once or within a short period of time. Females of some synchronously ovulating squids have been observed to carry their egg masses in pelagic waters; this phenomenon is known as "post-spawning egg care" or "egg brooding" and has been observed for *Gonatus onyx* Young, 1972 (Seibel et al., 2005), *Gonatus madokai* Kubodera and Okutani, 1977 (Bower et al., 2012), *Gonatopsis* spp. (Okutani et al., 1995) and *Bathyteuthis berryi* Roper, 1968 (Bush et al., 2012). Remains of egg masses have also been found on trawl-captured specimens of *Gonatus fabricii* and *Gonatus antarcticus* Lönnberg, 1898, suggesting that these species likely also brood their eggs (Arkhipkin and Bjørke, 1999; Hoving, 2008; Laptikhovsky et al., 2007). Deep-sea benthic incirrate octopods produce large eggs (10–30 mm) and have low fecundity (up to a few hundred oocytes) (e.g. Barratt et al., 2007; Laptikhovsky, 2013). Although some studies have suggested that some deep-sea incirrate octopods could possibly be multiple spawners (Barratt et al., 2007), Laptikhovsky (2013) recently demonstrated, by identifying the postovulatory follicles, that females of deep-sea incirrates probably spawn a single egg mass simultaneously or a series of several small batches over a short period of time (1–3 weeks). The same study suggested that the evolution of this strategy among deep-sea incirrates might be associated with the costs of parental care, a common strategy within these cephalopods (Voight, 2008; Voight and Grehan, 2000).

Deep-sea cephalopods produce a wide range of egg sizes and numbers (e.g. Laptikhovsky, 2013; Laptikhovsky et al., 2007, 2008), with deep-sea and polar incirrates at the high end of the size spectrum, having among the largest eggs known for any invertebrate (generally 10–30 mm, Laptikhovsky, 2013; up to 41.5 mm in length; Allcock et al., 2003). Large squids like *Architeuthis* and *Dosidicus* produce millions of small eggs (~2 mm and ~1 mm, respectively) and are repeated spawners, having the highest fecundities of all cephalopods (e.g. Hoving et al., 2004; Nigmatullin and Markaida, 2009). Among deep-sea cephalopods, pelagic brooding species (squids and octopods) and benthic cephalopods (octopods) produce larger eggs than pelagic repeated spawners. This trend also seems to be true within families. For example, *Heteroteuthis dispar*, a pelagic squid from the family Sepiolidae (which has mainly truly benthic species), produces significantly more and smaller eggs than similarly sized and even larger species in the family (Hoving et al., 2008b). Similarly, pelagic octopods like *Argonauta* produce more and smaller eggs than *Muusoctopus* spp., a genus of benthic octopod species from the same suborder (Laptikhovsky, 2001; Laptikhovsky and Salman, 2003). Cirrate octopods have intermediate sizes and number of eggs, compared to *Muusoctopus* and *Argonauta* (Laptikhovsky, 2001; Laptikhovsky and Salman, 2003), which may be related to their continuous-spawning strategy (Villanueva, 1992). Egg size and fecundity seem inversely correlated, and fecundity is related to body size, with cephalopods only capable of spawning as many eggs as the coelomic cavity can hold. Therefore, repeated spawners can increase their actual fecundity compared to synchronous spawners (Laptikhovsky et al., 2007).

5.2. Age analysis and longevity

Cephalopod longevity has implications for many other aspects of these animals' biology and evolution, but the impracticality of making direct observations in most instances has required the development of other means for inferring life-cycle length.

One technique is to keep individuals alive in the laboratory; this approach is very valuable but also very difficult, especially for deep-sea taxa. To date, to our knowledge, only one study has successfully tracked the growth rate of a living deep-sea cephalopod in the lab: O'Dor and Malacaster (1983) maintained *Bathypolypus arcturi* and reported low growth-rate estimates (0.18 % body mass/day) and a relatively high longevity (>4 years) for this species compared to other neritic octopods.

The age of an individual cephalopod may be determined postmortem by quantifying increments in its hard body structures. By determining the ages of individuals of a wide variety of sizes, it is possible to reconstruct growth curves and estimate longevity. Structures useful for age determination of individual cephalopods must meet three criteria: (1) they must contain "interpretable increment structures that are sufficiently clear to facilitate precise interpretation," (2) "the increment structure is able to be correlated with a regular and determinable time scale," and (3) the incremented parts continue "to grow at a measurable rate throughout the life of the cephalopod" (Beamish and McFarlane, 1983 from Arkhipkin, 2005). In cephalopods, statoliths, gladii, stylets, beaks and eye lenses are all structures that meet the aforementioned criteria and will be discussed in the succeeding text.

Statoliths (calcium carbonate concretions located in the statocysts, the cephalopod's organs of balance) are the most widely used structures to estimate age at size in squid. Hurley et al. (1979) and Lipinski (1979) provided the first evidence of daily deposition of statolith increments, confirming their potential as proxies for individual squid age. Their periodic growth, which is correlated with growth of the animal, results in the formation of increments, which can be counted using microscopy. However, the periodicity of statolith increment formation requires validation (e.g. Lipinski, 1986; Lipinski et al., 1998); at present, deposition is known to occur daily in several ommastrephid species (Arkhipkin, 2004), in the oceanic squid *Onychoteuthis borealijaponica* Okada, 1927 (Bigelow, 1994) and in juveniles of the oceanic squid *Abralia trigonura* Berry, 1913 (Bigelow, 1992). These species comprise a very small proportion of the known oegopsid squid taxa (24 families, 69 genera and 206 currently described species; ToLweb Young and Vecchione, 2004), but this is not surprising as validation studies, although necessary, require husbandry of living deep-sea cephalopods.

Oceanic squid age estimations based on statolith increments suggest a wide range of lifespans for different taxa (see Arkhipkin, 2004 for review). Small squids of the families Enoploteuthidae and Pyroteuthidae appear to have life cycles that are completed in less than 6 months (Arkhipkin, 1996a; Young and Mangold, 1994). Larger enoploteuthids and small ommastrephids (8–15 cm ML) also live for approximately half a year (references in Arkhipkin, 2004). Larger ommastrephids (*Sthenoteuthis pteropus* Steenstrup, 1855, and *S. oualaniensis* Lesson, 1830) and *Thysanoteuthis rhombus* each appear to have a 1-year lifespan (Arkhipkin and Mikheev, 1992; Nigmatullin et al., 1995).

Other oceanic squids seem to live longer and grow more slowly. Female *Ancistrocheirus lesueuri* mature at about 2 years and reach a mantle length of ~400 mm (Arkhipkin, 1997). On the South Atlantic continental slope of South Africa, female *Lycoteuthis lorigera* reach maturity around 11 months (ML 100 mm) and have been estimated to live for 1 year (Hoving et al., 2007), while *Histioteuthis miranda* Berry, 1918, from the same area may live for up to 2 years (Hoving and Lipinski, 2009).

While counting statolith increments can be a powerful tool for investigating the life-cycle length—and other aspects of ecology (migration, ontogeny, etc.; Arkhipkin, 2005) of some deepwater squid—their interpretation has also resulted in some questionable age estimations. If daily deposition occurs in the giant squid, *Architeuthis*, the total number of statolith increments suggests extremely high growth rates and ages of just 1–2 years for large animals of 975–2168 mm ML (e.g. Gauldie et al., 1994; Lordan et al., 1998; Roeleveld and Lipinski, 1991; review O'Shea, 2004a). Age estimations of *Architeuthis* based on other body structures (eye lenses and gladii), or using theoretical predictions, suggest a longer lifespan (Grist and Jackson, 2007; O'Shea, 2004a). The one-increment-per-day hypothesis should thus be tested for as many squid species as possible, in particular from different families.

In some cephalopods, statoliths are not suitable for quantification of increments. In *Vampyroteuthis infernalis*, for example, the statolith is not a solid concretion, but just crystals loosely clinging together (H.J. Hoving, personal observation). In octopods, the statoliths appear to have no increments and are soft and "chalklike" (Clarke, 1978), so other structures should be investigated for suitability in age determination.

The shell in squid, the gladius (or "pen"), provides quantifiable increments in both juvenile and post-juvenile phases of some species (Arkhipkin and Perez, 1998). Validation experiments have shown that these increments (in the ostracum) are also laid down daily in some oceanic squid species (e.g. *Illex*, Perez et al., 1996; Schroeder and Perez, 2013), but it has not yet been possible to calculate total age. One advantage of using the gladius for age estimation is that the structure size is directly related to the size of the squid, allowing reconstruction of individual growth rates and trajectories. These have allowed, for example, the identification of important growth shifts during the life history of *Illex illecebrosus*, as the animal transitions from oceanic to neritic environments in the Northwest Atlantic (Perez and O'Dor, 2000). Conversely, a disadvantage is that early increments are subsequently overgrown and can therefore be unreadable. The gladius is also a good alternative when statolith increments become faint and unreadable, a process that happens particularly in larger squid (e.g. *Onykia robusta* (Verrill, 1876); Bizikov and Arkhipkin, 1997). In *Architeuthis* from New Zealand, six large increments in the gladius have been found, which could potentially indicate an age of 6 years (O'Shea, 2004a).

Incirrate octopods do not have gladii; some species instead have vestigial shell remnants called stylets, which are two very fine, elongate structures in the mantle muscle at the base of the gills (Bizikov, 2008; Wells, 1978). Concentric rings have been observed in sectioned stylets, and experiments where individuals were exposed to a fluorescent marker that becomes incorporated into the stylet indicate that these, too, form daily (Doubleday et al., 2006; Hermosilla et al., 2010). However, assuming daily deposition of stylet increments, specimens of the deepwater octopod *Bathypolypus sponsalis* were estimated to be <1 year old (Barratt and Allcock, 2010), which does not agree with the longer lifespan (3–4 years) suggested by laboratory-kept individuals (O'Dor and Malacaster, 1983). A very large deepwater octopod, *Megaleledone setebos* Robson, 1932, was estimated to attain an age of 3–4 years (potentially including embryonic development) based on the number of increments in the stylets (Barratt and Allcock, 2010).

Doubleday and Semmens (2011), using the shallow-water octopod *Octopus pallidus* Hoyle, 1885, found that the age pigment lipofuscin (visible in brain tissue using standard histological techniques) is highly exponentially correlated with age in laboratory-reared animals. Because the age determined by stylets corresponded well with the age estimations from lipofuscin quantification, this method may have potential as an alternative ageing method for octopus and perhaps other deep-sea cephalopods.

Structures that may prove particularly valuable in ageing cephalopods, but which have received relatively little scientific attention thus far, are the growth increments in cephalopod beaks. Beaks are present in all cephalopods, and their species-specific morphology can be used for identification (Clarke, 1986). Daily deposition of increments in the beaks has been validated for adult *Octopus vulgaris* Cuvier, 1797 (Canali et al., 2011; Oosthuizen, 2003; Perales-Raya et al., 2010), and this method has now been successfully applied to assess the growth differences in wild populations of *O. vulgaris* (Perales-Raya et al., 2013). Quantification of increments in the beaks of squid for the purpose of age estimation has only been studied for the deep-sea squid *Onykia ingens* (Clarke, 1965). Growth increments have been observed in the beaks of the deep-sea squids *Liocranchia reinhardtii* Steenstrup, 1856, and *Chiroteuthis* cf. *veranyi* Ferussac, 1835 (Franco-Santos and Vidal, 2014). However, one potential drawback to using beaks for ageing is the fact that feeding causes structural wear, especially in voraciously predatory cephalopods.

Age estimation could also be accomplished using the cephalopod eye lens, which develops before hatching and grows throughout the individual's life, and shows visible growth increments in cross section (Baqueiro Cárdenas et al., 2011; O'Shea, 2004a). In *Architeuthis*, the total number of rings in one eye lens suggested (assuming daily formation) an age of 6.1 years in an individual of ML 1845 mm (O'Shea, 2004a). The low variation found in eye lens growth in *O. vulgaris*, contrary to highly variable mantle length/body mass relationships, suggests that it may also be a suitable structure to use for age estimations in octopods (Baqueiro Cárdenas et al., 2011).

In addition to providing insight into overall longevity, some of these structures may also allow more specific life-history inferences to be drawn. For example, microstructure of the statolith can sometimes suggest the duration of various life-cycle stages. Species of the family Cranchiidae have been suggested to spend the first part of their life (~6 months) in epi- and mesopelagic waters, after which they descend into the bathypelagic to mature (Arkhipkin, 1996b,c). *Gonatus onyx* lives at least 2 years before reproducing (Hunt and Seibel, 2000) in the bathypelagic, and then females brood the eggs (whose development is slow, due to low temperatures at bathypelagic depths) for up to 6–9 months (Seibel et al., 2005). Therefore, the brooding time, combined with maturation time, suggests a total lifespan of approximately 3 years, at least for females. Using the model on cephalopod embryogenesis developed by Laptikhovsky (2001), the development time for *Gonatus fabricii* eggs was estimated to be 12 months, based on the size of the eggs (approximately 4–6 mm) and the temperature of Arctic bathypelagic waters (−0.7 to 0.8 °C) (Arkhipkin and Bjørke, 1999). Similarly, *Bathyteuthis berryi* embryos are estimated to require 12 months to reach a TL of 5 mm at 2–4 °C (Bush et al., 2012). These findings indicate that the brooding times for some bathypelagic cephalopods are longer than the complete life cycles of some coastal and epipelagic squids (e.g. Jackson, 2004).

Other indications of deepwater cephalopods' longevity can be derived from chemical analyses of body tissues. The digestive gland of *Architeuthis* from the Bay of Biscay showed increased levels of cadmium, compared with other smaller mesopelagic squids and even higher compared to neritic species (Bustamante et al., 2008). Such levels could mean that *Architeuthis* preys upon taxa that are more contaminated than the prey of other mesopelagic squid, or that giant squid live longer than other cephalopods, allowing higher concentrations of contamination to accumulate (Bustamante et al., 2008). Isotopic analysis of body tissues from Tasmanian giant squid has suggested an age of 14 years (ML 1910–2400 cm) (Landman et al., 2004).

5.3. Trophic ecology

Oceanic squids of the families Ommastrephidae, Gonatidae and Onychoteuthidae are known for their versatile predatory feeding behaviour. Their high metabolic requirements, the generally short life cycle and the semelparous life-history strategy demand a high nutritional intake (Rodhouse and Nigmatullin, 1996). Therefore, it is not surprising that these animals feed on a wide variety of prey from pelagic crustaceans to fish to other cephalopods, which they may catch at night in surface waters after undertaking diel migrations from deeper strata (Table 3.5). This opportunism often includes cannibalism, which sometimes forms a significant dietary component in species such as *Dosidicus gigas* (Ibañez and Keyl, 2010). Cannibalism is often a response to stress (Ibañez et al., 2008), particularly during fishing operations (Markaida and Sosa-Nishizaki, 2003), and so may be overestimated in some cases, but it also appears to emerge as a natural strategy when food is scarce (Maurer and Bowman, 1985). Smaller examples of opportunistic predators likely include members of the enoploteuthid families. For example, *Watasenia scintillans* is known to prey upon crustaceans and pelagic fish (Hayashi, 1995).

Since these nektonic predators may hunt within the water column as well as near (or even on) the sea floor, versatility is required in body morphology, particularly structures involved in prey capture and feeding. The agility and strong swimming abilities of many oceanic cephalopods allow the capture of fast-moving prey (O'Dor and Shadwick, 1989), and the brachial crown (arms and tentacles) in many squid species also allows for the efficient capture of a wide range of prey sizes and types (Packard, 1972). A tremendous morphological diversity has also evolved among the armature of these structures (sucker rings and hooks), likely facilitating the capture and handling of prey (Engeser and Clarke, 1988; Nixon and Dilly, 1977).

Table 3.5 Diets of selected deep-sea cephalopods

Higher classification	Species	Size (mm) (male/ female)	Dietary components	Reference
Order Octopoda				
Suborder Incirrata				
Family Amphitretidae	*Japetella diaphana*	100	Crustaceans (euphausiids, copepods)	Passarella and Hopkins (1991)
Family Alloposidae	*Haliphron atlanticus*	4000 TL	Crustaceans, cnidarians	Willassen (1986) and O'Shea (2004b)
Family Octopodidae	*Graneledone boreopacifica*	145	Molluscs, crustaceans	Voight (2000)
	Megaleledone setebos	280	Ophiuroids, amphipods, fish	Piatkowski (unpublished)
	Pareledone charcoti	70	Crustaceans mainly	Piatkowski (unpublished)
	Pareledone turqueti	120	Benthos	Piatkowski (unpublished)
	Vulcanoctopus hydrothermalis	50	Polychaetes, amphipods, other crustaceans	González et al. (1998), Rocha et al. (2002), and Voight (2005)
Suborder Cirrata				
Family Opisthoteuthidae	*Opisthoteuthis californiana*	90	Small crustaceans, polychaetes	Pereyra (1965)
	Opisthoteuthis calypso	100	Crustaceans, polychaetes, gastropods	Villanueva and Guerra (1991)
	Stauroteuthis syrtensis	350	Copepods (mostly *Calanus finmarchicus*)	Jacoby et al. (2009)
Order Sepiolida				
Family Sepiolidae	*Rossia macrosoma*	85	Benthos, shrimp	Mangold-Wirz (1963)

Continued

Table 3.5 Diets of selected deep-sea cephalopods—cont'd

Higher classification	Species	Size (mm) (male/ female)	Dietary components	Reference
Order Teuthoidea				
Family Architeuthidae	*Architeuthis dux*	<3000	Fish, squid, crustaceans	Peréz-Gándaras and Guerra (1978), Förch (1998), Lordan et al. (1998), and Bolstad and O'Shea (2004)
Family Chiroteuthidae	*Chiroteuthis veranyi*	200	Pelagic small crustaceans, mollucs, fish	Kubota et al. (1981)
	Grimalditeuthis bonplandi	250	Cephalopods, crustaceans	Hoving et al. (2013b)
Family Cranchiidae	*Galiteuthis glacialis*	<190	Zooplankton, euphausiids (Antarctic krill)	Rodhouse and Piatkowski (1995)
Family Enoploteuthidae	*Abralia redfeldi*	30	Copepods, euphausiids	Passarella and Hopkins (1991)
	Abraliopsis atlantica	33	Copepods, euphausiids	Passarella and Hopkins (1991)
	Watasenia scintillans	70/60	Shrimp, planktonic crustaceans, pelagic fish	Hayashi (1995)
Family Gonatidae	*Berryteuthis magister*	430	Fish, squid, pelagic crustaceans, large zooplankton	Kuznetsova and Fedorets (1987) and Nesis (1997)
	Berryteuthis anonychus	150	Crustacean zooplankton, fish	Uchikawa et al. (2004)
	Gonatopsis borealis	300/280	Pelagic crustaceans, fish, squid, zooplankton	Reviewed in Roper et al. (2010a,b)

Table 3.5 Diets of selected deep-sea cephalopods—cont'd

Higher classification	Species	Size (mm) (male/female)	Dietary components	Reference
	Gonatus fabricii	385	Fish, pteropods, chaetognaths, cephalopods, crustaceans	Kristensen (1984) and Wiborg et al. (1984)
Family Histioteuthidae	*Histioteuthis bonnellii*	330	Mysids, shrimp, zooplankton, mesopelagic fish	Quetglas et al. (2010) and Fanelli et al. (2012)
	Histioteuthis reversa	200	Myctophid fish, pelagic crustaceans, cephalopods	Quetglas et al. (2010)
	Histioteuthis miranda	260/270	Crustaceans	Clarke (1980)
	Histioteuthis corona corona	190/170	Copepods and euphausiids	Passarella and Hopkins (1991)
	Histioteuthis celetaria pacifica	280/230	Crustaceans and fish	Voss (1962) from Voss et al. (1998)
	Histioteuthis arcturi	130/210	Copepods and euphausiids	Passarella and Hopkins (1991)
Family Lycoteuthidae	*Lycoteuthis lorigera*	190	Pelagic crustaceans and myctophids	Voss (1962) and Lipinski (1992)
Family Ommastrephidae	*Dosidicus gigas*	1200	Epi- and mesopelagic fish, squid, shrimp, euphausiids, cannibalism	Braid et al. (2012) Nigmatullin et al. (2001), Markaida (2006, 2008), and Hoving et al. (2013a)
	Hyaloteuthis pelagica	105	Juvenile pelagic fish and squid, crustaceans	reviewed in Roper et al. (2010a,b)

Continued

Table 3.5 Diets of selected deep-sea cephalopods—cont'd

Higher classification	Species	Size (mm) (male/female)	Dietary components	Reference
	Illex argentinus	400	Fish, squid, crustaceans (mostly euphausiids)	Ivanovic and Brunetti (1994) and Laptikhovsky (2002)
	Illex coindetii	379/279	Fish, crustaceans, cephalopods, gastropods	Rasero et al. (1996) and Sánchez et al. (1998)
	Illex illecebrosus	340/270	Mostly fish and pelagic crustaceans	Froerman (1984) and O'Dor and Shadwick (1989)
	Martialia hyadesi	400	Euphausiids, mesopelagic fish	González et al. (1997) and Dickson et al. (2004)
	Nototodarus sloanii	420	Crustaceans (euphausiids), fish, squid	reviewed in Roper et al. (2010a,b)
	Ommastrephes bartramii	420/900	Squid, fish (mostly myctophids), shrimp, cannibalism	Lipinski and Linkowski (1988), Seki (1993), and Watanabe et al. (2004)
	Ornithoteuthis antillarum	300	Crustaceans, fish, chaetognaths, squid	Arkhipkin et al. (1998)
	Sthenoteuthis oualaniensis	650	Mostly pelagic fish (myctophids), squid, shrimp	Shchetinnikov (1992), Snyder (1998), and Parry (2006)
	Sthenoteuthis pteropus	650	Mostly pelagic fish (myctophids), squid, shrimp	Reviewed in Zuyev et al. (2002)

Table 3.5 Diets of selected deep-sea cephalopods—cont'd

Higher classification	Species	Size (mm) (male/female)	Dietary components	Reference
	Todarodes angolensis	433	Mostly fish	Reviewed in Roper et al. (2010a,b)
	Todarodes filippovae	540	Fish, crustaceans, cephalopods	Reviewed in Roper et al. (2010a,b)
	Todarodes pacificus	500	Planktonic crustaceans, fish, squid	Okiyama (1965), Okutani (1983) and Song et al. (2006)
	Todarodes sagittatus	750/640	Fish, crustaceans, squid	Piatkowski et al. (1998), Quetglas et al. (1999), Lordan et al. (2001), and Fanelli et al. (2012)
Family Onychoteuthidae	*Ancistroteuthis lichtensteinii*	300	Fish and crustaceans (euphausiids)	reviewed in Roper and Jereb (2010) and Fanelli et al. (2012)
	Onychoteuthis banksii	370	Fish and squid	Arkhipkin and Nigmatullin (1997)
	Onychoteuthis borealijaponica	370/300	Small fish, squid	Okutani and Murata (1983)
	Onykia ingens	520	Euphausiids (Antarctic krill), mesopelagic fish, squid	Jackson et al. (1998) and Phillips et al. (2003a,b)
	Onykia robusta	2300	Benthic fish, echinoderms, jellyfish	Reviewed in Roper and Jereb (2010)

Continued

Table 3.5 Diets of selected deep-sea cephalopods—cont'd

Higher classification	Species	Size (mm) (male/ female)	Dietary components	Reference
Family Octopoteuthidae	*Taningia danae*	1700	Fish crustaceans	Santos et al. (2001) and González et al. (2003)
Family Pyroteuthidae	*Pterygioteuthis gemmata*	40	Copepods, euphausiids	Passarella and Hopkins (1991)
	Pyroteuthis margaritifera	50	Copepods, euphausiids	Passarella and Hopkins (1991)
Family Thysanoteuthidae	*Thysanoteuthis rhombus*	1300	Fish, squid	Nigmatullin and Arkhipkin (1998)
Order Vampyromorphida				
Family Vampyroteuthidae	*Vampyroteuthis infernalis*	22–210	(Remains of) gelatinous zooplankton, crustaceans (copepods, amphipods), detritus, remains of fish and squid	Hoving and Robison (2012)

Opportunistic feeding behaviour in some oceanic squids has also become apparent from stable isotope analysis (SIA) of body tissues. In SIA, an organism's carbon and nitrogen stable isotope signatures are assumed to be influenced by what it has consumed (e.g. Kelly, 2000). In the marine environment, stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are indicators of the main feeding areas and trophic levels of consumers, respectively (Cherel and Hobson, 2005). Stable isotope analysis can also provide information on the habitat in which the individual has grown and hence yields clues to migration behaviour and habitat utilization (e.g. Cherel and Hobson, 2005; Jackson et al., 2007; Ruiz-Cooley et al., 2013).

In cephalopods, SIA has been performed on various body structures, including the mantle, beaks, gladii, arms, eye lenses and digestive glands (e.g. Cherel and Hobson, 2005; Jackson et al., 2007). Using SIA on *Dosidicus gigas* muscle tissue and gladii, for example, small individuals have been found to migrate into the northern California Current System from different regions to feed and grow (Ruiz-Cooley et al., 2013). High-resolution sampling of metabolically inactive body structures like gladii ("with no metabolic turnover after synthesis" as per Lorrain et al., 2011) may provide other information on dietary preferences and trophic position throughout ontogeny. In another study on *D. gigas*, stable isotope signatures were analysed along the gladius, revealing that this species does not necessarily increase its trophic level with age, showing that individual squid have a highly varied diet, are flexible in their feeding strategy, and migrate actively (Lorrain et al., 2011). A potentially unusual trend was identified using cephalopod beaks retrieved from stomachs of dead emperor penguin chicks at Pointe Géologie, Terre Adélie, Antarctica: varying δ^{15}N signatures in the onychoteuthid *Kondakovia longimana* showed that larger individuals of this squid tended to source prey from lower in the food web than smaller individuals, suggesting a dietary shift from fish to euphausiids during growth (Zimmer et al., 2007).

Fatty-acid analysis is another technique that can reveal valuable information on trophic position and diet but that has rarely been used for deep-sea cephalopods to date (Rosa et al., 2013b). Fatty-acid analysis utilizes the fact that certain fatty acids can only be biosynthesized by phytoplankton and macroalga species, which have distinct ratios in fatty acids that influence the ratios of fatty acids in consumers and thus give information on position in the food web (Graeve et al., 2002). Individual fatty acids or groups of fatty acids may also be related to prey type or species. The combination of fatty-acid analysis and stomach-content analysis can enable detection of temporal and spatial variations in feeding and also recognition of specific prey items that cause temporal differences in uptake of dietary lipids. In the onychoteuthid *Onykia ingens*, fatty acids analysed from the digestive gland have revealed dietary differences among regions, seasons and years, which were attributed to a dietary change from myctophids to crustaceans (Phillips et al., 2003a,b). In another study, distribution and lipid composition were studied in the Antarctic cranchiid squid *Galiteuthis glacialis* Chun, 1906 (Piatkowski and Hagen, 1994). Storage lipids (triacylglycerols) were found to be low, comprising 18–26% of total lipid, which in turn made; the latter made up only 8–11% of the dry weight, which reflected the early developmental stage of the specimens examined.

In many oceanic cephalopod families, some or all species accumulate ammonium in their tissues to increase buoyancy (see Voight et al., 1994 for review); these are called "ammoniacal cephalopods." Although some ammoniacal cephalopods are obviously very strong swimmers (e.g. Octopoteuthidae), many ammoniacal species have reduced metabolic rates and swimming capabilities (e.g. Seibel and Drazen, 2007; Seibel et al., 1997, 2004). Histioteuthids, an ammoniacal family, are known to ingest typical cephalopod prey like crustaceans, fishes and cephalopods (Table 3.5) but overall diet information on ammoniacal squid is virtually absent.

Species that certainly have a less active lifestyle are the cephalopods that have adopted an ambush-predatory (or "sit-and-wait") feeding strategy. Squids of the family Chiroteuthidae have large, robust ventral arms, with sheaths into which the very long tentacles that can be retracted (Young and Roper, 2011c). The large tentacle club is equipped with many small suckers and a distal photophore; photophores are also present along the length of the tentacle stalk. In *Chiroteuthis calyx* Young, 1972, the tentacle has been observed to be deployed and retracted, presumably to capture midwater fish (Robison, 2004).

In the same family, *Grimalditeuthis bonplandi* has tentacles that presently appear to be unique among cephalopods: the stalks are very thin and the clubs bear no armature or photophores (Hoving et al., 2013b; Young et al., 1998). ROV observations show that the club swims out from the brachial crown by undulating movements and, when positioned at some distance from the squid, is manoeuvred in such a way that it resembles the movement of a small organism. This apparently lures other cephalopods and crustaceans to within reach of the arms (Hoving et al., 2013b), demonstrating a feeding strategy known as aggressive mimicry or luring (Wickler, 1965). Mastigoteuthids, the "whiplash" squids, have been observed by ROV to hover above the sea floor with their tentacles extended just millimetres off the bottom (Roper and Vecchione, 1997). The tentacles of most species bear numerous tiny (sometimes microscopic) suckers, which are presumably used to capture copepods or perhaps larger prey (Roper and Vecchione, 1997). Magnapinnids, the "bigfin" squids, are an elusive family of deep-sea cephalopods that have only been observed below 2000 m. These squids possess exceedingly long, slender extensions of all arms, which are deployed below the squid and may be several metres long (Vecchione et al., 2001), and appear to be highly adhesive. The function of this modification is unknown but may well be related to feeding.

Deep-sea octopods also show a great variety of feeding strategies. A comprehensive review of the main prey found in stomachs of cirrate octopods was provided by Collins and Villanueva (2006, their table 7). Small crustaceans, such as gammarid amphipods, mysids, copepods, isopods and decapods, and polychaetes and bivalves are the most abundant prey items (e.g. Collins, 2003; Collins and Villanueva, 2006; Vecchione and Young, 1997; Villanueva and Guerra, 1991). Most of these studies concluded that epibenthic and benthopelagic feeding seem to be very common (Vecchione, 1987; Villanueva and Guerra, 1991). Additionally, fatty-acid analysis has revealed a benthic detrital feeding strategy in the cirrate *Opisthoteuthis calypso* Villanueva, Collins, Sanchez and Voss, 2002 (Rosa et al., 2013b). The only direct observations on the feeding behaviour of cirrate octopods were reported from laboratory studies of *Grimpoteuthis* sp. (Hunt, 1999), which exhibited three distinct feeding modes in the laboratory: envelopment of the prey (*Artemia* nauplii), entrapment and current feeding by movement of the cirri. The large pelagic incirrate octopus *Haliphron atlanticus* apparently feeds on crustaceans and cnidarians (O'Shea, 2004b; Willassen, 1986). Among the bottom-dwelling incirrate deep-sea octopods, *Graneledone* cf. *boreopacifica* and *Vulcanoctopus hydrothermalis* prey upon gastropods, polychaetes and crustaceans (González et al., 1998; Rocha et al., 2002; Voight, 2000), with the latter species also feeding on swarming amphipods by engulfing with the arms, a strategy apparently specialized to target one particular species of amphipod *Halice hesmonectes* (Voight, 2005). Another deep-sea octopod that seems to specialize in a single prey item is *Stauroteuthis syrtensis* Verrill, 1879, which was found to prey solely on the copepod *Calanus finmarchicus* (Jacoby et al., 2009) (Table 3.5).

A particularly peculiar feeding behaviour has recently been described for *Vampyroteuthis infernalis*. This species was observed (by ROV) to extend its retractile filament, which may be up to 9 × the body length (Hoving and Robison, 2012). Under laboratory conditions, food particles were found to adhere to this filament, which is equipped with microscopic hairs; the food-laden filament was then withdrawn between the arms and the food was removed and later observed as a clump in the beak (Hoving and Robison, 2012). Additional ROV observations repeatedly showed vampire squid with clumps of food in their beaks. Stomach-content analysis revealed a variety of zooplankton, crustacean moults, faecal pellets from copepods, amphipods and larvaceans, gelatinous material and incidental fragments of fish and squid that appeared to have been scavenged, based on isolated occurrence (Hoving and Robison, 2012). Larger macerated prey items such as fishes or crustaceans, which are typical of many other deep-sea cephalopods and require active hunting, were never observed. It therefore appears that vampire squid feed on already-dead, decomposing material from the water column and may opportunistically ingest copepods and other crustaceans, either dead or alive. Recent studies suggest that the ram's horn squid *Spirula spirula* is another cephalopod that ingests detrital material and marine snow (Ohkouchi et al., 2013); as mentioned in the preceding text, a third instance of benthic detrital feeding has been reported in the cirrate *Opisthoteuthis calypso* (Rosa et al., 2013b).

Although SIA and fatty-acid analysis have proven to be valuable tools in dietary analysis, they may lead to confusing results when used without other lines of evidence. For example, SIA on cephalopod beaks sourced from stomach contents of various predators from the subantarctic Crozet and Kerguelen archipelagos and Adélie Land, Antarctica, revealed a cephalopod diversity of 18 species spanning three trophic levels (Cherel and Hobson, 2005). Interestingly, the largest cephalopods did not necessarily occupy the highest trophic position, that is, body size was independent from the stable isotope ratios of nitrogen. For example, *Chiroteuthis veranyi* was positioned higher in the food web than the giant squid *Architeuthis dux* (Cherel and Hobson, 2005). SIA should therefore preferably be used in combination with stomach-content analysis. Visual identification of stomach contents, however, is time consuming and difficult; cephalopods macerate their food considerably, sometimes making identification nearly impossible.

DNA sequencing of prey tissue recovered from stomachs may help with this problem. Although this method is rather elaborate and a library of potential prey items needs to be available for comparison, when used, it can reveal interesting insights into deep-sea cephalopod diet, for example, cannibalism in giant squid (Deagle et al., 2005, confirming earlier reports by Bolstad and O'Shea, 2004) and *Vampyroteuthis infernalis* ingesting pieces of *Gonatopsis borealis* (Hoving and Robison, 2012). The advantage of direct identification (visual or via DNA sequencing) is that the results provide an instant insight into recently consumed food items. Stomach-content analysis, however, may be biased by the phenomenon of "net feeding," where cephalopods under stress begin consuming any nearby organism (Markaida and Sosa-Nishizaki, 2003; Rodhouse and Nigmatullin, 1996). Therefore, stomach-content analysis of deep-sea cephalopods that have been captured by ROV (e.g. Hoving and Robison, 2012) may provide a more unbiased source of dietary data and should be investigated where possible in future studies.

The diets of many species are likely to change ontogenetically, but relatively few studies have compared diets across different life stages to date.

The limited available data have shown interesting and dramatic changes in dietary preferences and morphology of feeding-associated structures. In *Architeuthis*, δ^{15}N profiles of beaks have indicated an early-life dietary shift, although the exact diet composition of early life stages of *Architeuthis* remains unknown (Guerra et al., 2010). Stable isotope analysis on eye lenses of the gonatid *Berryteuthis magister* (Berry, 1913) revealed an increase by one trophic level from juvenile to adult stages (Hunsicker et al., 2010). In addition to these dietary shifts, major morphological modifications have also been observed in some species. For example, in the cranchiid *Galiteuthis glacialis*, probable adaptive allometry of the brachial crown has been discussed as a response to the general increase of pelagic prey size with depth (Rodhouse and Piatkowski, 1995). Doratopsid paralarvae of the Chiroteuthidae differ radically from the subadult and adult forms (Sweeney et al., 1992; Vecchione et al., 1992), and the mechanics and function of this metamorphosis remain unknown. Interestingly, one exception seems to be the vampire squid, whose feeding apparatus in the juvenile form is almost identical to that of the adult (Young and Vecchione, 1999).

Forage locations (benthic vs. pelagic or geographical area) adopted during different cephalopod life stages may also be detected via SIA. Pelagic cephalopod species (e.g. histioteuthids and *Vampyroteuthis infernalis*) are reported to have carbon-depleted tissues and structures, while benthic cephalopods (e.g. *Bathypolypus sponsalis*) are generally enriched in carbon (Cherel et al., 2009; Fanelli et al., 2012). Two of the 18 species examined in Kerguelen waters (*Architeuthis* and the brachioteuthid *Slosarczykovia circum-antarctica* (Lipinski, 2001) were found to have spent considerable time in waters outside Kerguelen (Cherel and Hobson, 2005).

Large deep-sea squid are rarely collected or encountered in adequate numbers to achieve a good representative idea of their feeding strategies. However, the piecemeal insights that has been reported provides some interesting information. One individual of the poorly known mastigoteuthid *Idioteuthis cordiformis* (Chun, 1908) had remains of snapper (*Lutjanus* sp.) and birdbeak dogfish (*Deania calcea*) in its stomach (Braid, 2013). *Onykia robusta* has been reported to feed on benthic fish and echinoderms, as well as on the pleustonic jellyfish *Velella velella* (from Jereb and Roper, 2010). Examined stomach contents of the giant squid *Architeuthis dux* have contained benthic prey such as octopods and the Norway lobster *Nephrops norvegicus*, among other pelagic prey such as whiting and squid (probably remains of histioteuthids, onychoteuthids and ommastrephids; Bolstad and O'Shea, 2004; Förch, 1998; Lordan et al., 1998; Peréz-Gándaras and

Guerra, 1978) (Table 3.5). Several specimens of the "colossal" squid *Mesonychoteuthis hamiltoni* have been captured by longliners targeting Patagonian toothfish (*Dissostichus eleginoides*), but whether this is its natural prey remains uncertain.

6. DISCUSSION AND CONCLUSIONS

Deep-sea cephalopods have been recognized and studied for hundreds of years, and although much information remains to be gathered, many techniques for researching these animals have been developed. Great advances have already been made in the twenty-first century, with a number of these species having been observed alive in their natural habitats for the first time within just the past decade. However, deep-sea cephalopods remain difficult to collect and observe, even with large deep-sea sampling gear like double-warped trawls and advanced observation equipment such as ROVs. Every sampling device has advantages and disadvantages, and collection tools should be used in combination where possible to obtain a more complete understanding of the true community composition of any deep-sea habitat. Tools that can only observe cannot replace nets as samples are required for validation of observations and also for further biological analysis. On the other hand observational tools are crucial for providing insight into behaviour and microhabitat and also for the collection of living cephalopods for experiments. Nets cannot do this. Ideal cephalopod survey methods use a combination of observational tools that can also collect (e.g. ROVs with collection devices) and nets that can also observe (e.g. cameras integrated onto nets). Predators can provide useful corroborative data on deep-sea cephalopods (e.g. distribution, role in the food web and the location and capture of large and sexually mature specimens in particular), but studies on teuthophagous animals' feeding ecology require input from experts on cephalopod systematics, especially when using beaks. Existing museum collections of cephalopods are another important resource for the research community, but only if there is awareness of their holdings and location. Rare specimens housed in these institutions may be used to substantiate otherwise small data sets, for example, for stomach-content analysis (e.g. *Vampyroteuthis infernalis* Hoving and Robison, 2012; *Grimalditeuthis bonplandi* Hoving et al., 2013b) and morphological and taxonomic studies. Museum specimens also have great value for testing hypotheses based on in-situ observations and vice versa (Hoving and Vecchione, 2012; Hoving et al., 2012). Archived in situ observations on deep-sea cephalopods via different initiatives are now complementing the vast number of museum specimens housed in worldwide collections, and it is important to note that the value of each is greatly increased by the other. Utilizing these two data sources in concert can greatly increase the knowledge gained from both, and this interplay of resources can only become stronger and more productive in the future.

The paucity of fossil cephalopods means that much information about the phylogeny and evolution of this class must be inferred from studies of extant groups. Once consistent systematic information is gained, processed and accepted for many recent deep-sea cephalopod taxa, researchers may be able to interpret fossil records more successfully and better understand some of the many unresolved evolutionary questions. To this end, scientific cruises using a variety of collection and monitoring techniques are needed in the areas where major gaps exist worldwide, such as the Arctic, southwest Atlantic, Indian and Pacific Oceans. Material from these regions would yield additional morphological and genetic information for known taxa (and would probably reveal new taxa), adding important data to our still-incomplete understanding of cephalopod biogeography and systematics. With a relatively small number of species, compared to other animal groups, it may even be feasible for the whole class to be eventually examined using both morphology and DNA sequencing—techniques that should be used in concert for systematic work wherever possible. Improvements in DNA extraction from formalin-fixed tissue, particularly the buccal mass, may also enable new data to be gathered from the vast museum holdings of recently and historically collected cephalopod specimens worldwide.

Like many habitats on Earth, the deep-sea environment is changing physically and chemically. Understanding the phylogenetic linkages among cephalopods is imperative in order to understand the physiological and behavioural patterns observed within family groups and to predict how they may react to large-scale global events such as climate change.

One of many exciting challenges in deep-sea cephalopod research is exploring the pelagic or "deep water." Only a fraction of this, the largest biome on Earth, has been explored (Ramirez-Llodra et al., 2010). In particular, the bathypelagic (the ocean layer between 1000 and 3000 m) may provide new insights into cephalopod biology. This habitat may hold the key to encountering and understanding mature life stages and egg masses of deep-sea cephalopods; brooding female squids have been observed here (Bush et al., 2012; Seibel et al., 2005) and, as so few egg masses have ever been observed, other nonbrooding species may spawn here too. However, fully understanding the biology of many deep-sea taxa requires an understanding of photic-zone communities as well, given the commonly observed life-history strategies of ontogenetic descent and diel vertical migration in these animals.

Recent insights into reproductive strategies, tactics and behaviours of deep-sea cephalopods have shown interesting patterns that are radically different from those of well-studied coastal species. One of the key remaining questions is whether (and to what extent) the evolution of reproductive strategies in deep-sea cephalopods has been driven by habitat-related pressures. Understanding the interplay of distinct selective pressures that potentially influence the evolution of cephalopod reproductive biology will certainly require an integrative approach, including studies on phylogeny, life history and genetics as well as experimentation.

Methods for investigating trophic position, longevity and age–size comparisons in neritic species should be applied to deep-sea cephalopods in order to investigate how their life cycles differ from their shallow-water counterparts. An open question in deep-sea cephalopod biology is whether (and in what taxa) growth increments in various hard body structures may provide a proxy for age. Basic data on size-at-age trends are lacking for the majority of squid species, in part because validation (which requires the husbandry of deep-sea cephalopods) is necessary for trustworthy age estimations. Fortunately, advances in collecting living cephalopods using ROVs have allowed for improvements in husbandry and experimental designs for investigating deep-sea cephalopods (e.g. Hoving and Robison, 2012; Hunt, 1999; Robison et al., 2003). Significant progress has also been made in techniques for culturing cephalopods in the last three decades, which could serve as the foundation for technological improvements in rearing deep-sea cephalopods. If successful, captive observations could greatly enhance our ability to gain information on these animals' biology and life cycles (Vidal et al., 2014, this volume).

Although proof is accumulating that deep-sea cephalopods occupy a wide range of trophic levels, for many species and in some cases whole families, dietary information remains completely unknown. One particular combination of techniques that should be more widely applied is the traditional identification of stomach contents (visually or using molecular tools) and analysis of stable isotopes and fatty acids of body tissues. From the data that are accumulating, it seems that deep-sea cephalopods have evolved diverse feeding strategies and range from the typical, opportunistically feeding strong swimmers, to sit-and-wait predators (which in some cases may even deploy lures), to planktivores to detritivores.

While future research efforts on deep-sea habitats will likely result in exciting discoveries on deep-sea cephalopods, there is also reason for concern. Examples of change in the ocean environment and anthropogenic impacts that may influence deep-sea cephalopods include expanding hypoxia, ocean acidification, pollution, deep-ocean warming, low-frequency anthropogenic noise and deep-sea fishing (e.g. Balmaseda et al., 2013; Gilly et al., 2013; Morato et al., 2006; Seibel et al., 2004; Solé et al., 2011, 2013; Unger et al., 2008). With increasing fishing pressure on deep-sea fish stocks, high numbers of nontarget species may also be captured, including cephalopods; for example, deep-sea bottom trawling may have resulted in regional extinction for some cephalopods in New Zealand waters (Freeman et al., 2010). Another consequence of deep-sea fishing may be that cephalopods expand into the niches of exploited and removed fish, a phenomenon that has been hypothesized for several squid species (e.g. Zeidberg and Robison, 2007). Deep-sea cephalopods are also vectors of persistent anthropogenic pollutants: relatively high levels of flame retardants have been measured in deep-sea cephalopods from >2500 m (Unger et al., 2008) and mercury concentrations in the tissue of some specimens of the giant squid *Architeuthis* have been found to be higher than has been reported in any coastal cephalopod species (Bustamante et al., 2008). In addition, low-frequency anthropogenic noise similar to that produced in the marine environment by shipping, acoustic exploration and deep-sea drilling has been shown to affect neritic and oceanic cephalopods in the lab (Solé et al., 2011, 2013) and has been hypothesized to impact deep-sea species in their natural environment also (Guerra et al., 2004). Most recently, Golikov et al. (2013) examined the distribution of cephalopods in the Arctic region and found extensive geographical range extensions of deep-sea cephalopods and attributed this to warming of the Arctic.

Understanding the biology of these animals under both current and potential future conditions will require ongoing dedication, innovation and collaboration. Much of the research will need to be interdisciplinary in nature, linking cephalopod researchers with colleagues from other fields, such as predator ecologists, oceanographers and fisheries biologists. Many major gaps remain in our knowledge of deep-sea cephalopods, including (but not limited to) basic biology (reproduction and life cycle), basic ecology (distribution, abundance and availability to predators) and trophic roles, at various temporal and spatial scales. These gaps can eventually be filled, but only by using the collective expertise and resources of the greater cephalopod research community and by keeping abreast of technological advances that may improve sampling and observational capabilities.

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APPENDIX A. WORKING LIST OF CEPHALOPOD COLLECTIONS

Acronym	Institution (* indicates online database available)	Location
AM	Australian Museum*	Sydney, Australia
ANSP	Academy of Natural Sciences*	Philadelphia, PA, the United States
ARC	Atlantic Reference Centre*	St. Andrews, Canada
BMNH	Natural History Museum*	London, the United Kingdom
BPBM	Bernice Pauahi Bishop Museum*	Honolulu, HI, the United States
CASIZ	California Academy of Sciences, Invertebrate Zoology*	San Francisco, CA, the United States
CBR	Colecciones Biológicas de Referencia*, Institut de Ciències del Mar	Barcelona, Spain

CMN	Canadian Museum of Nature	Ottawa, Canada
FMHU	Hokkaido University Museum	Hakodate, Japan
FMNH	Field Museum of Natural History	Chicago, IL, the United States
NTM (formerly FMT)	National Taiwan Museum	Taipei, Taiwan
FURG	Universidade Federal do Rio Grande	Rio Grande, Brazil
FWRI	Florida Wildlife Research Institute*	St. Petersburg, FL, the United States
IMAS (formerly IASOS)	Institute for Marine and Antarctic Studies	Hobart, Australia
IRSNB	Institut Royal des Sciences Naturelles de Belgique*	Brussels, Belgium
JAMSTEC	Japan Agency for Marine-Earth Science and Technology*	Yokosuka, Japan
LIPI	Indonesian Institute of Sciences	Jakarta, Indonesia
LKCNHM (formerly NMS, RMBR)	Lee Kong Chian Natural History Museum, National University of Singapore	Singapore
LS	Linnaean Society	London, the United Kingdom
MCZ	Museum of Comparative Zoology, Harvard University*	Cambridge, MA, the United States
MfN (formerly ZMB)	Museum für Naturkunde*	Berlin, Germany
MFRDB (formerly MFDT)	Marine Fisheries Research and Development Bureau, Department of Fisheries	Bangkok, Thailand
MHNG	Muséum d'Histoire Naturelle de la Ville de Genève	Geneva, Switzerland
MMI	Museum of Marine Invertebrates, University of Puerto Rico, Mayagüez*	Isla Magüeyes, Puerto Rico
MNCN	Museo Nacional de Ciencias Naturales*	Madrid, Spain
MNHN	Muséum National d'Histoire Naturelle*	Paris, France

MOM	Musée Océanographique de Monaco	Monte Carlo, Monaco
MSUT (formerly FUMT)	University Museum, University of Tokyo*	Tokyo, Japan
MV	Museum Victoria*	Melbourne, Australia
MZUSP	Museu de Zoologia da Universidade de São Paulo	São Paulo, Brazil
MZUS	Musée Zoologique de la Ville de Strasbourg, University of Strasbourg	Strasbourg, France
NCB (merger of RMNH, ZMA)	Naturalis Biodiversity Center	Leiden, the Netherlands
NIWA	National Institute of Water and Atmospheric Research, Ltd*	Wellington, New Zealand
NMNH (formerly USNM)	National Museum of Natural History, Smithsonian Institution*	Washington, DC, the United States
NMNZ	National Museum of New Zealand Te Papa Tongarewa*	Wellington, New Zealand
NMSIB (formerly NMSZ)	National Museums Scotland, Invertebrate Biology*	Edinburgh, the United Kingdom
NRM	Naturhistoriska Riksmuseet (Swedish Museum of Natural History)	Stockholm, Sweden
NMNS (formerly NSMT)	National Museum of Nature and Science*	Tokyo, Japan
PIFSC	Pacific Islands Fisheries Science Center, National Marine Fisheries Service	Honolulu, HI, the United States
RSMAS (formerly UMML)	Invertebrate Museum, Rosenstiel School of Marine & Atmospheric Science, University of Miami	Miami, FL, the United States
SAM	South African Museum	Cape Town, South Africa
SBMNH	Santa Barbara Museum of Natural History*	Santa Barbara, CA, the United States
SIO	Scripps Institute of Oceanography	La Jolla, CA, the United States
SMF	Senckenberg Forschungsinstitut und Naturmuseum (Senckenberg Museum, Frankfurt)	Frankfurt, Germany

SZN	Stazione Zoologica Anton Dohrn di Napoli*	Naples, Italy
UMUB (formerly ZMUB)	University Museum, University of Bergen	Bergen, Norway
WAM	Western Australian Museum	Perth, Australia
ZIN	Zoological Institute of the Russian Academy of Sciences	St. Petersburg, Russia
ZMH	Zoologisches Museum, Universität Hamburg	Hamburg, Germany
ZMMGU	Zoological Museum, Moscow State University	Moscow, Russia
ZMUC	Zoological Museum, University of Copenhagen	Copenhagen, Denmark
ZSI	National Zoological Collections, Zoological Survey of India	Kolkata, India

APPENDIX B. RECENT AND ONGOING SURVEYS

Ongoing surveys open to collection requests

Nature and location	**Contact**
Live Hawaiian bobtail squid (*Euprymna*) collected via dipnet in Oahu, Hawaii, shipped live to Wisconsin, the United States, and maintained	N. Bekiares squidroom@gmail.com
Caribbean cephalopods collected from by-catch; specimens retained at MMI	N. Schizas n_schizas@cima.uprm.edu
Atlantis Project: targets cephalopods as well as recovery from by-catch, Falkland Islands and SW Atlantic; retained at the Spanish Institute of Oceanography, Vigo	J. Portela julio.portela@vi.ieo.es
Trawl, by-catch, ROV capture (via *Alvin*) and donation programmes from the eastern Pacific off North and Central America; specimens retained at FMNH	J. Voight jvoight@fieldmuseum.org
Hawaii Institution of Marine Biology targets *Octopus oliveri* and *O. cyanea*, intertidal and shallow reef by hand; specimens retained at HIMB	H. Ylitalo hyw@hawaii.edu

Instituto Português do Mar e da Atmosfera collects cephalopod by-catch from Portugese Groundfish Survey; specimens retained at IPMA	J. Pereira jpereira@ipma.pt
Consejo Superior de Investigaciones Científicas works with biodiversity surveys, deep-sea sampling, groundfish by-catch and donations from the northeastern Atlantic; specimens retained at CSIC	R. Villanueva roger@icm.csic.es
Museum of Aquatic Organisms (FURG) targets cephalopods via diving, trawl net and recovery from by-catch and predators, southwestern Atlantic	T. Silva Leite leite_ts@yahoo.com.br
LIPI, CASIZ undertake a variety of collection programmes, via trawl, ROV, hand lines and by-catch recovery, equatorial Pacific and Southern Ocean; specimens retained at LIPI, CASIZ, SBMNH and BPBM. Openness to sampling depends on organization and cruise	Various

Recently completed surveys

Nature and location	Contact
Cephalopod paralarvae targeted via bongo and neuston nets, 0–200 m, Gulf of California and eastern Pacific off Mexico, 1996–1998, 2003–2007, 2010; specimens retained at the Departamento de Plancton y Ecología Marina, Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN), La Paz, México	R. De Silva Dávila rdesilva@ipn.mx
Mesopelagic and bathypelagic cephalopods targeted via midwater trawl, Gully Marine Protected Area, northwestern Atlantic, 2007–2010; specimens retained at Delaware Museum of Natural History.	E. Kenchington ellen.kenchington@dfo-mpo.gc.ca
Pelagic and benthic cephalopods targeted via trawl during the MAR-ECO cruises along the Mid-Atlantic Ridge, North Atlantic, 2004; specimens deposited at UMUB	E. Willassen endre.willassen@um.uib.no

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