

Chapter 2

Behaviour

Jennifer Mather and David Scheel

Abstract The coleoid cephalopods, typified by cuttlefish, squid, and octopuses, are carnivorous molluscs. Of the better-known coastal cephalopods, many live in shallow water, are short-lived, physiologically efficient, and nocturnal. The behaviour of cephalopods overall is poorly known: a basic ethogram is available for one cuttlefish and one octopus species. Cuttlefish and squid eat primarily fish and crustaceans; the octopus diet includes crustaceans and molluscs. Most cephalopods prefer live natural food and prepared diets reduce growth compared to natural food. Cephalopods are generally solitary. A semelparous life history, parental care of eggs only in the octopuses (and a few squid) and no overlap of generations restrict the opportunity for social behaviour. Cuttlefish reproductive tactics may be complex, and squid swim with conspecifics in schools. Smaller cephalopods are at risk for cannibalism from larger ones (common in 59% of species and high in 24%). Cephalopods use visual displays, and some have size-based social hierarchies in captivity. Coastal coleoid cephalopods grow rapidly (live only 1–2 years), mature at an early age, and many die shortly after laying eggs. Many species of squid and cuttlefish aggregate for spawning, while male octopuses locate receptive females by chemoreception. Most young hatch at a small size, are planktonic, and must hunt live appropriate-sized prey. Major challenges to mariculture include keeping tiny planktonic paralarvae alive, providing adequate diet for growth, and avoiding cannibalism within high density captive populations.

Keywords Behaviour · Cephalopods · Life history · Diet · Antipredator · Reproduction

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Table 2.1 Aspects of the behaviour of the three major cephalopod groups^a

Behaviour	Cuttlefish	Squid	Octopus
Habitat choice	Benthic, semi-benthic	Pelagic	Benthic
Sensory	Vision, chemical	Vision, mechanical	Vision, chemical
Locomotion	Jet	Jet	Crawl/jet
Antipredator	Camouflage, hiding, ink	Jet escape, ink	Hiding, camouflage, ink
Skin displays	Camouflage, sexual	Sexual	Camouflage
Prey	Fish, crustacean	Fish	Mollusc, crustacean
Sociality	Social at reproduction	Social groups	Solitary
Care of young	None	None	Female egg brooding

^a Many minor exceptions

2.1 Introduction

Behaviour is one of the most simple and obvious aspects of the life of any animal. But besides being easy to see, it has logical links to the ecology of animals' interactions with their surroundings and the physiology of their internal workings (Drickamer et al. 1996). Generating an environment that allows a captive cephalopod to express its normal range of behaviour, such as providing shelter for cuttlefish and octopuses, and space for squid, is important for their health and competence. But behaviour can also be used as a cue of trouble. Unusual coloration, poor muscle tone, change in feeding behaviour, or location in an atypical place or position can tell the people keeping the cephalopods that something is wrong.

There are two problems with describing the behaviour of 'the cephalopod'. The first one is that there is a large number of species, normally inhabiting and adapted to a wide variety of marine habitats (see Table 2.1). The abundant coleoid cephalopods are typified by cuttlefish, squid, and octopuses, many of which live in shallow water, are short-lived, semelparous, and physiologically efficient though not necessarily active more than 25% of the time (Mather 1988). The few nautiloids, represented by *Nautilus* and *Allonautilus* (see Chap. 10), are long-lived iteroparous inhabitants of the cold depths.

Some cephalopods, such as the octopuses, seem 'preadapted' to confinement (Boycott 1954), occupying a sheltered 'home' for around 70% of the time (Mather et al. 1985; Mather 1988). In contrast, the jet-propelled squid in their normal pelagic environment are typified by *Sepioteuthis sepioidea*, who make a startle jet escape at an average of eight times per hour, moving a mode of 2 m distance (Mather 2010), a difficult response in a laboratory environment.

A second problem with describing the behaviour of cephalopods is that it is poorly known, though see Hanlon and Messenger (1996) for an excellent but somewhat dated summary. A basic ethogram (description of the common behaviour of a species) can only be pieced together for *Octopus vulgaris*—see Wells' (1978) and Mather et al.'s (2010a) popular books—and *Sepia officinalis* (see Guerra 2006), though the behaviour of the latter has not been studied in the wild. Squid and cuttlefish species often gather to mate and their agonistic and sexual behaviour is fairly well known (Hall and Hanlon 2002; Hanlon et al. 2002; Jantzen and Havenhand

2003a, b) but descriptions of the rest of their behavioural repertoire are lacking. Many cephalopods are nocturnally active and their activity cycle is not flexible (Meisel et al. 2006), though again *O. vulgaris* is the exception. The behaviour of nocturnal animal is difficult to study, as shining a light on them can change their behaviour and few scientists have a night-viewing system that works in the water.

Nevertheless, the behaviour of cephalopods can reveal basic adaptations to the necessities of life. The first necessity is adapting to the physical, chemical, and biological environment around them, including predators. Although predators may be absent in a laboratory environment, antipredator reactions such as inking will still be present. The second necessity is provision of food, and although the laboratory environment may provide food easily, there are the problems of appropriate diet, food preparation, and enrichment with food provision for young. A third necessity is relationship with conspecifics; although many of the cephalopods are not social (Boal 2006), this can bring problems for confinement itself, such as cannibalism (Ibáñez and Keyl 2010). A fourth necessity is provision of opportunities for reproduction, from the stage of mating through guarding of eggs in octopuses to the provision of a proper environment for planktonic paralarvae (see Chap. 23). Understanding these problems can lead to providing an enriched environment for cephalopods in captivity. Enrichment of the captive environment is not just window-dressing for aquarium audiences (Peters et al. 2005). Cuttlefish raised in an enriched environment grow faster and learn better (Dickel et al. 2000) and habitat enrichment increases the activity and widens the range of skin patterns in mudflat octopuses (Biegel and Boal 2006). This is particularly important for development, as young cuttlefish given a complex background learn to produce skin patterns and dig in the sand more quickly (Poirier et al. 2004, 2005). Taking these aspects of biology into consideration, Moltschanivskyj et al. (2007) have written a thorough review of ethical and welfare considerations when keeping cephalopods.

2.2 Antipredator Behaviours

Without the protection of the molluscan shell, cephalopods are at risk for predation, particularly from fish (Packard 1972). They have evolved a galaxy of antipredator responses, including skin displays mediated by the complex chromatophore system (Messenger 2001). Excellent bottom-matching camouflage (Hanlon and Messenger 1988) is a specialty of the cuttlefish and this matching has been used to investigate the ability of the cephalopod visual system to analyse its environment (e.g. Barbosa et al. 2008). Young nektonic squid such as *S. sepioidea* use a variety of patterns accompanied by postures to match features of their environment (Moynihan and Rodaniche 1977; Mather et al. 2010b). In the open water, many squid and cuttlefish use reflexive countershading for camouflage from predators above or below (Ferguson et al. 1994). On the approach of a potential predator, cephalopods of all groups use startle deimatic displays with eyespots (Langridge et al. 2007; Mather 2010; Staudinger et al. 2012). These are selectively used in the presence of visual

predators (Langridge et al. 2007) and are directed towards an approaching potential predator (Mather 2010), though not to an imminent danger. Octopuses (*Octopus cyanea*) escaping from a scuba diver following them may use unpredictable pattern changes (Hanlon et al. 1999b) and eventually escape. Similarly, young cuttlefish (Hanlon and Messenger 1988), *S. sepioidea* (Mather et al. 2010b), and *Euprymna scolopes* (Anderson and Mather 1996) use a combination of an unpredictable sequence of moves to different locations, pattern and posture change and ejection of a squid-sized ‘dummy’ dark blob (see Hanlon and Messenger 1996 for discussion).

The primary response of octopuses is hiding (Mather 1994). The provision of even a pair of bricks in the laboratory evokes this response, and an octopus not given such material may cower arms outward in the corner of a tank. Such a shelter can also be provided in the form of an open cube or a pot, which is very useful for transport of a captive animal with the minimum amount of handling stress. Given more material, however, octopuses will manipulate it to form a shape they prefer. In the wild, octopuses can hide in shells, human discards such as beer bottles (Anderson et al. 1999), crevices, and under rocks. They do not find the ‘ideal’ home in terms of characteristics such as volume and aperture area, but instead modify shelter by clearing out sand and rubble, detaching algal fronds, and bringing rocks to block the aperture (Mather 1994). Many octopus species are likely limited in the wild by the availability of shelter (see Hartwick et al. 1978 for *Enteroctopus dofleini*). Cuttlefish and other sepiolids (Mather 1986; Anderson et al. 2004) bury themselves in sand if they are provided with small grain size and an adequate depth. Squid primarily use jet-propelled escape responses (O’Dor and Webber 1986).

Most cephalopods have the ability to release ink during a major threat, and do so in combination with escape and appearance change. This may deter predators by either blocking their chemoreception (Wood et al. 2010) or impeding their vision. Ink can be dispersed in the sea as a screen or held together as a ‘dummy’ (Anderson and Mather 1996). Ink can also become an alarm cue to conspecifics (Wood et al. 2008). Given its efficacy, it is surprisingly rarely used, but a replacement must be metabolized for future threats if ink is lost by ejection. Increased or maximal initial threat eventually causes escape responses in most cephalopods. In the laboratory, many of the display responses are harmless and seldom seen; eyespots seem to be the exception. But jet escape responses can lead to posterior mantle skin damage (Hanlon et al. 1983) and ink circulating in a restricted tank environment can damage the health of cephalopods and any other animals in the same system.

2.3 Foods and Feeding Behaviours

All cephalopods are carnivores, and most exhibit a preference for live natural foods. These factors have constrained the aquaculture of cephalopods and are part of the current challenge of improving aquaculture methods, particularly for early life stages where mortality is the highest (e.g. Vaz-Pires et al. 2004; Sykes et al. 2006; Uriarte et al. 2011). In the wild, cephalopods may forage solitarily, as cuttlefish and

octopuses typically do, or in aggregate, as may squid (Neill and Cullen 1974; Boal 2006), although many schooling squid forage solitarily at night. The coleoid cephalopods are visually guided predators, although octopuses may also forage tactilely (for review, see Hanlon and Messenger 1996). For many cephalopods, hard remains of prey—from stomach contents for squid and from midden piles outside the den for octopuses—provide information about diet composition. Diet remains much less well known from deep water species, away from dens, or from soft prey whose remains are not found in middens or stomach, although that is changing as information from molecular methods becomes available (e.g. Lorrain et al. 2011). However, in such cases, molecular data have confirmed that descriptions of diet content from hard remains include the majority of cephalopod prey (e.g. Stowasser et al. 2006; Hunsicker et al. 2010; Lorrain et al. 2011), although some molecular methods may provide greater temporal detail (e.g. Hunsicker et al. 2010).

2.3.1 Cuttlefish (Order Sepiida) and Squid (Order Teuthida)

The main foods of cuttlefish and squid are shrimp, crab, and fish, but they also are known to consume other crustaceans (euphasiids, copepods, cirripedes, amphipods), some molluscs (including gastropods, bivalves, and cephalopods), as well as polychaetes (Hanlon and Messenger 1996). Knowledge of squid-feeding ecology is limited (Lorrain et al. 2011). Squid are active predators whose total dietary composition is broad and varies with growth. Among *Illex argentinus* individuals, 55–85% included crustaceans in their diet, mainly *Themisto gaudichaudii* (order Amphipoda) and euphasiids, while the occurrence of squid was 12–13%, and 3–29% of squid individuals consumed fish (Ivanovich and Brunetti 1994). Similarly, diets of common Atlantic squid *I. illecebrosus* and *Doryteuthis (Loligo) pealeii* were diverse, and while that of *I. illecebrosus* was dominated by fishes, squid, and non-decapod crustaceans, the stomach contents of *D. pealeii* consisted of largely unidentified prey remains, molluscs, and copepods (Bowman et al. 2000). Cannibalism occurs commonly and is increased by crowding (Ivanovich and Brunetti 1994; Ibáñez and Keyl 2010). Many squid are harvested by jigging (e.g. Chen et al. 2008) possibly indicating attacks to a wide range of stimuli that may contribute to a broad diet.

Both cuttlefish and squid attack prey in stages consisting of attention behaviours, a positioning approach, and ambush-like strike in which the long tentacles shoot out to seize the prey (Messenger 1968; Neill and Cullen 1974). The attention behaviours involve changes in body patterning, arm positioning, and orientation of the body towards the prey (Messenger 1968). For slower moving prey (such as crabs) of both squid and cuttlefish, approach occurs only from behind the prey, and seizure occurs with partially opened arms without use of the tentacles (Duval et al. 1984).

There is little work on the behavioural ecology of squid and cuttlefish diet choice, and these groups are considered predatory generalists (e.g. Guerra 2006). However, cuttlefish have been an important invertebrate model system to understand learning in the context of the ontogeny of hunting behaviour and prey choice (e.g. Messenger

1973; Dickel et al. 2000; Darmaillacq et al. 2004; Cole and Adamo 2005; Agin et al. 2006; Guibé et al. 2012). Within 24–48 h after hatching, cuttlefish strike at small suitable prey (Messenger 1973); attack latency, success rates, and suitability of potential prey items can be influenced by learning (e.g. Hanlon and Messenger 1996; Darmaillacq et al. 2004; Cole and Adamo 2005). Ontogenetic changes in prey selection also occur in squid, where adults may occupy a higher trophic level than smaller juveniles (e.g. Hunsicker et al. 2010; Ibáñez and Keyl 2010).

Squid depend on movement of prey items and contrast with the background to locate potential prey and elicit attack (Hanlon et al. 1983). Lacking these stimuli, especially motion, squid and cuttlefish will not attack and will starve to death. Prey size range does not appear critical, with both large and small squid taking prey ranging in size from macroplanktonic to nearly the same length as the squid itself (Hanlon et al. 1983). Squid orient visually towards their prey (Hanlon and Messenger 1996), as do cuttlefish, although cuttlefish also exhibit searching behaviour for partially buried prey in the substrate, which they uncover by expelling a jet of water over the substrate which can blow away cover (Hanlon and Messenger 1996). All squid are cannibalistic, a tendency enhanced under food shortage and in the presence of smaller or injured conspecifics. Further, mating behaviours such as male courtship of females and male–male aggression can disrupt feeding and may lead to injuries to fins or other areas that contribute to cannibalism (Hanlon 1990). Thus, feeding in captivity can be promoted and cannibalism reduced by keeping squid in tanks containing all individuals of the same size and sex.

2.3.2 *Octopuses*

The diets of a few species of octopuses are well known. Many species use dens in shallow water and discard hard remains of prey, including shells, carapaces, and bones, in midden piles outside the dens. The diet of shallow-water benthic octopuses is dominated by crustaceans (e.g. Mather et al. 2012) and molluscs such as bivalves (e.g. Vincent et al. 1998) and snails (Ambrose 1984). Diets typically are dominated by one to a handful of prey species, but diverse other prey occur occasionally in diets (e.g. Ambrose 1984; Scheel and Anderson 2012). Such occasional items may include alternative crustaceans or bivalves, but also almost any other prey group characterized by hard parts such as gastropods, chitons, cephalopods, echinoderms, fish, and even birds (Sazima and de Almeida 2006; Nightingail 2012; Scheel and Anderson 2012). Soft items (e.g. worms) may also be eaten but are less likely to be detected in the diet. In some populations, individual octopuses appear to exhibit prey specificity (Anderson et al. 2008b), although diet composition across the population is broad; in other populations, individual specialization appears not to be the rule (Mather 2011; Mather et al. 2012; Scheel and Anderson 2012; Leite et al. [in sub](#)).

Hard shells protecting crabs, bivalves, and other prey represent a challenge to octopuses' intent on feeding on the soft tissue inside, and octopuses have several methods to surmount this challenge. Marks left by octopuses on hard remains

of prey may indicate how the octopus handled the food item (*E. dofleini*: Dodge and Scheel 1999). Octopuses are known to apply strength alone to pull open prey (McQuaid 1994; Steer and Semmens 2003; Anderson and Mather 2007) so that not all remains from prey eaten by octopuses will be marked. Pulling may be the method of choice for some prey, especially bivalves (Steer and Semmens 2003), but pulling is not always successful. Octopuses are also well known for drilling through the shell of their prey, using salivary enzymes, papilla, and radula (Nixon and Maconnachie 1988). Drilling forms a small ovoid depression in the outer layer of the shell that penetrates the inner layer with holes 1.5–3.0 mm long and 0.25–2.0 mm wide (inner and outer width dimensions, respectively; Nixon and Maconnachie 1988; Dodge and Scheel 1999). Octopuses are known to drill hard shells and carapaces, as well as puncture softer tissue such as eyes (*Eledone cirrhosa*: Grisley et al. 1996). In some species of octopuses attacking bivalves, drill attempts consistently may be made in a location where the prey is vulnerable (Wodinsky 1969; Cortez et al. 1998; Anderson et al. 2008a). However, this does not appear universal and some octopus-drilled locations are variable or may be a function of prey type or size (*E. dofleini*: Dodge and Scheel 1999; Scheel et al. 2007). Alternatively, octopuses may chip prey with their beaks (Anderson 1994; Dodge and Scheel 1999) leaving characteristic marks on the edges of bivalves or breakage patterns on crab carapaces, chelae, or legs.

According to foraging theory (Pulliam 1974; Sih 1984; Stephens and Krebs 1986), diet selection by rate-maximizing foragers among spatially mixed prey types will be determined by prey energy content, handling time, and encounter rates. Spatial segregation of prey types may result in habitat selection influencing encounter rates and prey selection (Vincent et al. 1996). Alternatively, octopuses may act as risk-minimizing or time-minimizing foragers (Scheel et al. 2007; Leite et al. 2009). If so, this could result in a preference for larger prey (greater energy content) without regard for handling time. This seems particularly likely given the octopuses often consume food at a den or other shelter (Mather 1991a), and spend the majority of their time hiding (e.g. *O. vulgaris*: Mather 1988, *E. dofleini*: Scheel and Bisson 2012), which allows time to drill, chip, or pull open prey in safety (see Sect. 2.2). Scheel et al. (2007) and Scheel and Anderson (2012) found that *E. dofleini* exhibit a preference for larger prey individuals within a species, and for larger species among similar prey types (crustaceans). Preferences by this octopus species may further be influenced by detectability of the prey, possibly itself a function of prey camouflage behaviour, epiphytes, or escape responses. There is now a growing interest in examining the constraints octopuses may face in nutrient trade-offs (e.g. Lee 1994; Rigby and Sakurai 2004; Onthank and Cowles 2011) and their effects on diet, but research in this area is only beginning.

Few studies examine how octopuses choose where to forage or how they find food. *O. cyanea* conducts tactile, speculative, and saltatory foraging on shallow-water reefs (Yarnall 1969, Forsythe and Hanlon 1997), similar to speculative web-over foraging described for *E. dofleini* in shallow water (Johnson 1942, Cosgrove 2002). In both species, as well as *O. vulgaris*, foraging excursions may follow along habitat edges such as reef edges or cliff faces preferentially in habitats containing

suitable dens or other shelter (Mather 1991b; Forsythe and Hanlon 1997; Scheel and Bisson 2012; Smith 2012). Different species may forage at intervals from several times per day (*E. dofleini*: Mather et al. 1985; *O. vulgaris*: Mather 1991a) to every 2–3 days (*E. dofleini*: Scheel and Bisson 2012). Foraging trip lengths are generally small, extending no more than 30–57 m from a den for large species (*O. cyanea*: Ivey 2007; *E. dofleini*: Scheel and Bisson 2012) and to only 6 m for *O. vulgaris* (Mather 1994).

Octopuses and cuttlefish will take prepared foods, and there has been some effort to create prepared diets of both natural (e.g. shrimp, squid) and terrestrial (e.g. chicken) foods for rearing cephalopods in captivity (Lee et al. 1991; Lee 1994; Garcia et al. 2011; Rosas et al. 2011), with more recent work showing increased promise for solving this difficult problem. Although both cuttlefish and octopuses grew on prepared diets, in all cases growth rates were below those on natural foods, and in many cases cuttlefish and octopuses on prepared diets did not grow (Lee et al. 1991; Domingues et al. 2007; Domingues et al. 2008; Valverde et al. 2008; Rosas et al. 2011). Cuttlefish eating prepared foods exhibited lower assimilation efficiencies than on natural foods (Rosas et al. 2007), possibly in part due to interference with digestion by binders used in prepared foods (Rosas et al. 2008; Garcia et al. 2011). Live foods, especially for early developmental stages, continue to have more success than prepared diets. However, both cuttlefish and octopuses can readily be trained to take minimally processed but nonliving marine foods, such as fresh or frozen fish, squid, or shrimp (e.g. Koueta et al. 2006). Octopus growth rates may be higher on mixed than monotypic diets (Rigby and Sakurai 2004), and nutrition ratios may be important in maximizing growth (Lee 1994; Aguila et al. 2007; Onthank and Cowles 2011) although this remains poorly understood.

2.4 Nonsexual Social Interactions

A generalization that cephalopods are solitary outside of the reproductive period would be true, with small exceptions and some variation (Boal 2006). With a semelparous life history (see below), the presence of parental care only in the octopuses and a fairly complete lack of overlap of generations, cephalopods are not likely to have been selected for social behaviour. Cooperation would be selected for by three different mechanisms (Drickamer et al. 1996). One is mutualism, the benefit of interactions to both individuals, which is unlikely unless animals live in close proximity, like the squid. A second is kin selection, again unlikely when planktonic dispersal means that most cephalopods are not living near kin. A third is reciprocity, where one individual benefits another, expecting a future benefit, and again this is unlikely in animals such as cephalopods that avoid one another much of their lifetime. Nevertheless, social recognition occurs in some cephalopods (Boal 2006) and other social behaviours may occur but have yet to be carefully studied.

Outside of the reproductive period, cuttlefish may be solitary, although field data (Corner and Moore 1980) are fragmentary, and reproductive social tactics may have

been a selective force for cuttlefish intelligence (Brown et al. 2012). A size-based dominance hierarchy is true for older, though not newly hatched cuttlefish (Warnke 1994). Boal (1996) tackled the problem of social recognition through laboratory observations. She found that cuttlefish kept together in tanks did not react differently to familiar vs unfamiliar conspecifics and were not closer to familiar than unfamiliar ones. Given visual stimuli, they were more aroused (with a higher ventilation rate) by the sight of prey items than that of conspecifics (Boal and Ni 1996). When they were maintained in a small or a large tank, cuttlefish spaced themselves more widely in the large one and seldom approached to within two body lengths. In a small tank, there were more male agonistic zebra displays and more displacement of one animal by another (Boal et al. 1999). More importantly, cuttlefish in the large tank consumed 25% more shrimp prey, suggesting that the crowding in the small (1.5 m diameter for three animals) tank was stressful and that this stress was reducing food intake. This is not good news for anyone who wishes to cultivate cuttlefish in captivity; a more complex habitat may provide visual separation and reduce this stress.

Squid are different, in that they prefer to swim with conspecifics (Hurley 1978), in approximately parallel orientation and within a body length or two in captivity, even in a very large tank, 15 m in diameter (Mather and O'Dor 1984). Because the adults do not live after egg laying and the young are planktonic, again there is little likelihood of kin recognition. Most squid gather with conspecifics, though Moynihan and Rodaniche (1982) noted *S. sepioidea* swimming with *Doryteuthis (Loligo) plei*. Groups sort by size; although *S. sepioidea* are attracted to conspecifics whatever the size, smaller animals are at risk for cannibalism from larger ones and so maintain several body lengths distance. It has been suggested that squid on the end of a line are sentinels, watching for predators and escaping first from them (Hanlon and Messenger 1996). The presence of sentinels would suggest cooperative behaviour, where individuals would assume periods of excess risk and trade off this risk for better protection outside of their sentinel time (Drickamer et al. 1996). However, Adamo and Weichelt (1999) found that such sentinel behaviour was not true for *S. lessoniana*. With predator threat (Mather 2010) or when schools are larger (Mather and O'Dor 1984), squid more closely to one another, possibly monitoring spacing through water deformation received through their lateral line analogue (Budelmann and Bleckmann 1988). Like cuttlefish, many squid have visual displays, including mostly male agonistic ones (Di Marco and Hanlon 1997). In captivity, males set up a dominance hierarchy, with larger ones dominating smaller and winning agonistic interactions. But, as for cuttlefish (Warnke 1994) and octopuses (Mather 1980), the presence of a dominance hierarchy in a crowded situation does not prove any social recognition in the wider spaces of the natural environment.

Octopuses are perhaps the most solitary of cephalopods, with their density likely dictated by a lack of predator pressure rather than any mutual attraction. Such a lack can be direct, as when predators are excluded from a specific area (Aronson 1986 for *Octopus briareus*), or indirect, when shelter is limiting (for *E. dofleini*, Hartwick et al. 1978). Octopuses observed in the wild do not defend territories (Aronson 1986; Mather et al. 1985), although they may defend their immediate surroundings,

such as a sheltering home (Cigliano 1993). This lack of defence is accompanied by frequent moves from one to another small home range (Mather and O'Dor 1991). The exception may be *Abdopus aculeatus* (Huffard et al. 2008) which is known to gather at high densities in sea grass beds during reproduction. However, it is not known whether the animals are permanent or temporary occupants of these restricted areas. In the laboratory, octopuses may maintain dominance hierarchies based on size (Mather 1980). Cigliano's (1993) observations that with time, interactions may decrease, suggest recognition of this hierarchy. Tricario et al. (2011) have demonstrated the possibility of familiarity in *O. vulgaris*, but the flaws in the statistical analyses make it difficult to confirm.

The general lack of sociality in cephalopods may be one factor contributing to the frequency of cannibalism in the group. In their review of 34 species, Ibáñez and Keyl (2009) report cannibalism was common in 59% of species reported and high in 24%. The combination of little sociality with short lifespan, semelparous reproduction, and high metabolic rate may favour cannibalism. In the wild, it may contribute to population limitation, although for culture in the laboratory it is a major problem. In *I. illecebrosus* squid, cannibalism is found during high densities (O'Dor and Dawe 1998), and this is also true for *O. briareus* (Aronson 1983). It may be a response to a limited food supply, as in squid during migration (O'Dor and Dawe 1998), and some reports of cannibalism may be distorted due to stress during capture in fisheries. It is also size based, and where males and females are dimorphic in size, the larger sex may consume the smaller one.

Regardless of circumstances, cannibalism is a major problem for anyone keeping cephalopods in captivity. By definition, culturing animals means keeping them at high densities, which not only is stressful for them (Boal et al. 1999) but also creates a situation for consumption of animals by each other. To some extent, cannibalism can be avoided by keeping animals of the same size together, and since cannibalism is also partly dependent on food supply, it is useful to have a good supply of preferred food—which may be expensive and hard to procure (see discussion of food and feeding). Giving cephalopods a complex environment in captivity may maximize their ability to escape from conspecifics who would consume them, as well as increasing their growth and learning capacity (Dickel et al. 2000). Yet enrichment (Anderson and Wood 2001; Mather *in press*) is only a partial solution to the expression of normal behaviour in an unnatural environment.

2.5 Reproduction and Lifespan

2.5.1 Life History

Shallow-water coleoid cephalopods grow rapidly, mature at an early age, and are typically semelparous (but see below), dying shortly after laying eggs. Most cephalopods live only for 1–2 years (Boletzky 2003b; e.g. for *O. vulgaris*, Katsanevakis

and Verriopoulos 2006b). Thus, abundance is limited by juvenile recruitment rates rather than adult survival.

Adult size and age vary greatly. The smallest ones live just a few months (e.g. 3 months for the pygmy squid *Idiosepius* spp., Boletzky 2003b), while the largest ones (e.g. *E. dofleini*: Hartwick 1983) are associated with delayed maturity in cold-water habitats and growth to large size (Wood and O’Dor 2000; Farias et al. 2009). There is a stronger relationship of cephalopod lifespan with temperature than with body size (Wood and O’Dor 2000). The giant Pacific octopus, *E. dofleini*, is a cold-water species and unusual in living up to 5 years in captivity (Hartwick 1983).

2.5.2 Movement

A thorough review of cephalopod movement behaviours is beyond the scope of this chapter (see Semmons et al. 2007) but movement ecology has the potential to affect husbandry. Long-distance movements may occur for most sepiolids. *S. officinalis* makes seasonal onshore–offshore migrations (Guerra 2006), likely due to winter cooling of the waters. Cuttlefish, with their cuttlebone-based buoyancy mechanism, can also perform daily vertical migration—upward at night for food and downward in the daytime (Webber et al. 2000). Migration may also be site focused, as *Sepia apama* in Australia makes long-distance migration to gather in restricted areas for breeding (Hall and Hanlon 2002).

Squid are the most mobile cephalopods (see possible tracking techniques, Semmons et al. 2007). Not only do many species move metres back and forth over the short term (Mather 2010), they also gather in daytime in the shallows and disperse over deeper waters at night to feed (Hanlon and Messenger 1996). But larger and more open-ocean species may make huge lifetime movements. *I. illecebrosus* gathers to feed off the Grand Banks in northeastern North America; the adults may move offshore to mate and spawn and their eggs are encased in a large gelatinous capsule and drift south to off the southeast coast. There the eggs hatch and the young begin a northward journey (O’Dor and Dawe 1998). Similarly, *Dosidicus gigas* move southwards off the coast of South America to feeding grounds, then slowly back to their equatorial spawning grounds (Nesis 1983), with the newly hatched young dispersing westwards and drifting southeast. With global warming, their range is expanding northwards. Animals with movement patterns as far-ranging and complex as these will be difficult to raise in the confines of even a large laboratory setting.

While octopuses generally are amenable to confinement within a small environment when provided with a sheltering ‘home’, they eventually will attempt to leave. This may be tied to the octopus’ short-term occupation of small home ranges (Mather and O’Dor 1991; Scheel and Bisson 2012), as they only stay in a restricted area for days or weeks. Thus, there is a ‘laboratory lore’ of how to keep your octopus in the tank. Heavy weights on the lid, locking lids, and outdoor carpeting around the rim of the tank may act as deterrents. The likelihood of escape is somewhat different amongst species that have been kept in captivity, with *O. vulgaris* being the most likely one to escape (Wood and Anderson 2004). It is suggested though not

proven that an enriched environment, more space, and better nutritional state may keep the octopus confined. Still, some of them just want to leave. In the longer term, octopuses may make onshore–offshore migrations, perhaps for reproduction or to access a more appropriate food supply, but this may be irrelevant to their culture unless light level affects their reproduction.

2.5.3 *Semelparity*

Coastal cephalopods typically mature in about a year (Boyle and Boletzky 1996) and although many are semelparous, Rocha et al. (2001) have identified five different cephalopod reproductive strategies along a gradient in environmental stability, including four varieties of multiple spawning, three of which are nonterminal. Recognizing this complexity in cephalopod spawning behaviours has blurred the sharp distinction between semelparity and iteroparity. Cuttlefish lay individual or small groups of eggs and sequester them in protected spaces. They spawn intermittently over a period of several months. The squid deposit eggs in large egg masses, some seasonally in mass synchronized spawning events, and are typified by terminal spawning although there are some examples of nonterminal spawning (Rocha et al. 2001). According to Rocha et al. (2001), octopuses span the continuum between semelparity and iteroparity: Many shallow-water octopuses are small-egged species laying eggs in festoons or small clusters of a single spawning event, while deep-water octopuses such as *Graneledone* sp. but also some shallow-water octopuses (Anderson and Wood 2012) are large-egged species depositing eggs singly, perhaps over a protracted period. *E. megalocyathus* is an intermediate example (Ortiz 2006). In either case, females brood eggs over a long period and die after hatching of the young.

2.5.4 *Mating and Spawning*

Male cuttlefish court females, using multiple mating strategies (Norman et al. 1999), and deceive other males via female mimicry (Norman et al. 1999; Brown et al. 2012). Mass spawning is seen in the giant Australian cuttlefish, *S. apama* (Hall and Hanlon 2002). During these mass spawnings, both sexes have multiple mates; males defended females but not egg-laying sites, and males attempted takeovers of paired females through agonistic displays and attention to opportunities for extra-pair copulations via stealth or female mimicry (Hall and Hanlon 2002). Many aspects of this interaction, but not mass spawning, are typical of Sepiida.

S. officinalis males present a striped body pattern (intense zebra display) to other males; larger and darker males are dominant in such interactions (Boal 1997). However, females show consistent preference not for the larger or darker males, but for the most recently mated males and those showing fewer zebra displays (Boal 1997). She suggested that females used chemical cues rather than visual ones in assessing

males. In captivity, males may initiate copulation without obvious courtship (which females may avoid through escape responses), and male–male aggression occurs. The extent to which these behaviours are artefacts of spatial constraint in captivity is not known (Adamo et al. 2000) and may pose challenges for cultivation. Hanlon et al. (1999a) observed that males initiate mating in the head-to-head posture, and then direct jets of water on at the female's buccal membrane, likely to flush spermatangia placed there by previous mating, and then transfer their own spermatangia to the buccal membrane using the hectocotylus. The male then manipulates the spermatangium on the female to break it open so that sperm are released. Females appear to terminate mating and are then guarded briefly by the male.

Some squid species (e.g. *Loligo vulgaris*: Arnold 1990; *I. illecebrosus*: Hendrickson 2004) but not others (e.g. *D. gigas*: Nigmatullin et al. 2001) aggregate for spawning. Spawning grounds, e.g. for *L. reynaudii*, may be used repeatedly, spawning may not be synchronized within an entire population, and squid move between grounds over an extended period (Sauer et al. 2000). Nonetheless, spawning aggregations are harvested and support managed fisheries (Rodhouse 2001). In captivity, *L. vulgaris* mating behaviour and male–male aggression may be induced by the presence of a recently laid egg mass (or visually similar object) in the tank or even in the visual field (Arnold 1990), as well as by pheromones present in the egg mass (King et al. 2003; Cummins et al. 2011). Arnold (1990) observed that on detecting such an object, individual sexually mature squid investigate the object tactilely and may jet water at it (possibly an effort to flush away sperm from other males, see 'Cuttlefish' above). Males begin to dart about, display to other males, and place themselves between females and rival males. Females and males display to each other, accentuating oviducal gland and testes, respectively (*L. reynaudii*, Hanlon et al. 2002). A male will swim alongside a female and raise one or two medial arm in an S-shaped curved display posture. Dark bands or patches also feature in this display, especially in competition with rival males, who may also be chased (Byrne et al. 2003; Mather 2004). Male–male contests may also include physical contact such as fin beating (Hanlon et al. 2002). Social hierarchies determined via dominance in agnostic displays develop in captivity (Arnold 1990), while paired males have an advantage over intruder males in the wild (Hanlon et al. 2002), an effect due to female choice, as females jet to avoid unwanted male mating attempts. Copulation of paired *L. vulgaris*, described by Arnold (1990) and of *L. reynaudii* described by Hanlon et al. (2002), is preceded by the male positioning himself alongside but slightly below the female, flashing chromatophores. The male then grabs the female and positions his arms close to her mantle opening. He reaches into his mantle with his hectocotylus and picks up spermatophores, which are quickly ejaculated and cemented to the inside of the female mantle near the opening of the oviduct. The male then releases the female. Copulatory behaviour may be interspersed with egg laying, and newly released sperm may be observed on just-laid egg masses. Female choice may operate on several levels, including female manipulation of sex ratios, avoidance of mating attempts, and selection of stored sperm to fertilize eggs (Hanlon et al. 2002), leading to multiple paternity within egg strings (Shaw and Sauer 2004). Copulation alternated with egg laying will continue until

both sexes are exhausted. Squid die within hours. Sneaker males of *L. reynaudii* (Hanlon et al. 2002), as well as other squid (e.g. *D. gigas*: Nigmatullin et al. 2001) and cuttlefish (Hanlon et al. 1999a) mate in the head-to-head position. Mating behaviour may be variable and dependent on context (Hanlon et al. 2002; Jantzen and Havenhand 2003a). Thus, there are opportunities to manipulate the onset of spawning under cultivation, although courtship and mating behaviours may be inseparable from male–male aggression.

Male octopuses may use chemoreception to locate receptive females (Voight 1991a; Di Cristo et al. 2005). Populations may have a single (Ambrose 1988) or two (Katsanevakis and Verriopoulos 2006b) spawning (and hence recruitment) peaks per year, with post-settlement mortality rates >50% within 3 months. Octopuses are not territorial and males apparently do not guard receptive females (Voight 1991b; but for exception see Huffard et al. 2010). During precopulatory behaviours, the male approaches the female and extends the hectocotylus towards her. If not rebuffed, males touch the female with the ligula (which females may use in assessment of male maturity), and if receptive, females remain motionless (e.g. *Paroctopus digueti*: Voight 1991b). In some species, females also may approach males (in captivity, Cheng and Caldwell 2000), and males may not always distinguish between male and female potential mates, or even among species (Lutz and Voight 1994; Cheng and Caldwell 2000). Copulation then occurs in positions varying from at arm's length to the male engulfing the female beneath his web. The male inserts the hectocotylus into the female mantle cavity. Mating may last up to several hours and is typically terminated by the female (e.g. *Octopus joubini*: Mather 1978; *P. digueti*: Voight 1991b; *Hapalochlaena lunulata*: Cheng and Caldwell 2000). In at least some species, more complex male mating strategies may involve sneaker males, mate guarding, and competition (Huffard et al. 2008). Thus, aspects of mating, including male initiation of mating and mating technique, may depend on crowding or familiarity with territory (Mather 1978), and so mating under cultivation may differ from in the wild.

2.5.5 Egg-Care Behaviours

Cuttlefish selectively deposit their eggs on support, such as in crevices among appropriate corals (Boletzky 1998). Squid deposit their eggs, often en masse, on or under appropriate bottom substrate, such as in sand, under rocks, or on sessile organisms, anchor lines or other support, or in pelagic balloons (Oegopsids). Except for family Gonatidae and Bathyteuthida squid (Bush et al. 2012), neither squid nor cuttlefish are known to exhibit egg-brooding behaviours.

Most small-egged octopus species cement festoons of eggs to sheltered hard substrate, such as inside the roof of a den. Eggs are laid over several days. Females typically stop eating just before or about the time of egg laying, although this is not invariant. Females then tend eggs, manipulating each strand with arm tips and blowing jets of water across them. Dead eggs are removed, as may be any showing signs of fungi or algae (Batham 1957; Gabe 1975; Anderson and Wood 2012).

Females brood the eggs continuously and become increasingly pale during this period. When the eggs begin to hatch, the female may aid the process by manipulating the eggs. After paralarvae hatch, or in some cases before, when the female is completely spent, she will crawl out of her den and a short distance away to die. When a female dies prior to paralarvae hatching, her eggs may be quickly predated or overcome by algae and fungi.

2.5.6 *Hatching and Paralarvae*

Cuttlefish hatch as juveniles, without distinct paralarvae. Immediately after hatching, cuttlefish begin to learn to capture size-appropriate prey in a fashion similar to adults (e.g. Hanlon and Messenger 1988; Guibé et al. 2012). Cuttlefish hatch with fully differentiated tentacles and use these for prey capture from the start. In contrast, Teuthid squid also have no true larval form but some species do have an ecological and morphological paralarvae stage wherein they do not yet assume the adult form and lifestyle (Boletzky 2003a). Social interactions, such as schooling of adult Loliginid squid, do not occur in newly hatched cephalopods. Loliginid squid begin schooling several weeks after hatching and this continues into adult life (Boletzky 2003a). Like cuttlefish, Loliginid squid begin learning attack behaviours by experience, foraging immediately post hatching (Boletzky 2003a; Darmaillacq et al. 2008) but prey choice is partially cued prior to hatching. However, because Loliginid squid do not hatch with fully formed tentacles, their prey capture methods must change during ontogeny. For both of these cephalopod groups, hatchlings learn to position themselves appropriately to attack prey from a direction most likely to yield success, and to adopt different attack behaviours depending on the availability and density of both prey and competitors (Boletzky 2003a).

Octopus hatchlings will still have a remnant of the yolk sac attached that may sustain them for the first few days out of the egg. As for squid, hatchlings that do not yet have the adult form and lifestyle are termed paralarvae (Young and Harman 1988). These are planktonic, positively phototactic (causing them to swim upwards in the water column), and neustonic (orienting towards the water–air interface); at the ocean’s surface they hunt planktonic crustaceans and molluscs appropriate for their size. Prey are located visually (Villanueva et al. 1996) and must be provided at sufficient density and frequency to facilitate growth. Adequate nutrition for paralarvae of meroplanktonic octopus species poses one of the greatest challenges to cultivation. Paralarvae grow rapidly and move about by jetting (Villanueva et al. 1995). As they approach the size at which they settle, they may cling to floating objects (Nixon and Mangold 1996). Recruitment of meroplanktonic species to the benthic population is heavily influenced by oceanographic parameters including temperature influencing growth rate, and current patterns influencing retention and recruitment to the source population (Katsanevakis and Verriopoulos 2006a). Octopus hatchlings with adult form and lifestyle are termed juveniles, and these occur in the large-egged forms (Voight and Grehan 2000; Anderson and Wood 2012), many of which are found in deep sea. They adopt a

Table 2.2 Signs of problems with cephalopods in captivity

Cuttlefish	Semi-solitary
(Provide substrate for digging)	Not feeding
(Hiding in sand, daytime)	Lack of skin colour
	Not seeking shelter
	Abrasions on posterior, fin edges
	Poor posture
	Unresponsive to startle
	Buoyancy problems (floating)
Squid	Social
(Watch for escape response, jet collisions with tank)	Not feeding
	Lack of skin colour
	Separation from group
	Settled on substrate
	Abrasions on posterior, fins
	Unresponsive to startle
	Jerky, hesitant swimming
Octopod	Solitary
(Manipulation of substrate is normal)	Not feeding
(Prevent escape)	Lack of skin colour (except in sleep)
	Poor muscle tone (except in sleep)
	End of arms missing (not when previously acquired)
	Not seeking shelter (provide it)
	Unresponsive to startle

benthic lifestyle immediately, but also grow rapidly, feeding on crustaceans and other small prey (Forsythe 1984).

2.6 Conclusions

This chapter reveals how complex and poorly understood are the behaviours of cephalopods. Yet, despite this, knowledge of this natural behaviour can serve as a foundation for successful culture of different cephalopod species. Even this partial account gives details of limitations, suggestions for how to assure that animals thrive in captivity, and, perhaps most importantly, an indication of which behaviours to monitor to assure oneself that the animals are doing well or warning signs that they are in trouble (see Table 2.2). The major obstacles to successful cultivation remain keeping planktonic paralarvae alive, providing adequate diet for growth, and avoiding cannibalism within high density captive populations. Progress has been made in providing adequate diet, but no satisfactory solution is yet available on even this minimum requirement for successful mariculture.

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<http://www.springer.com/978-94-017-8647-8>

Cephalopod Culture

Iglesias, J.; Fuentes, L.; Villanueva, R. (Eds.)

2014, XIII, 494 p. 125 illus., 53 illus. in color., Hardcover

ISBN: 978-94-017-8647-8