Sussex IFCA
Inshore Fisheries and Conservation Authority

Supporting Sustainable Sepia Stocks

Report 1: The biology and ecology of the common cuttlefish (*Sepia officinalis*)

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Summary

The common cuttlefish *Sepia officinalis* L. 1758 is a marine mollusc within the class of cephalopoda. Cuttlefish are important predators, supplying top down predation control over a number of prey species. Cuttlefish are also prey to commercial species such as the Atlantic cod (*Gadus morhua*). Cuttlefish are intermittent terminal spawners. This means that they reproduce just once and then die at the end of their life cycle. They migrate inshore from their overwintering ground in the middle of the western English Channel to breed in coastal waters in the spring.

Historically, the English Channel population of the common cuttlefish was considered a non-target species for commercial fishers. This is no longer the case with many fishers diversifying into the cuttlefish fishery and catch rates increasing over the last decade.

This report describes in detail the biology and ecology of the common cuttlefish. This report was written as part of the Fisheries Local Action Group (FLAG) funded project; Supporting Sustainable Sepia Stocks. The other outputs from this project are:

- The English Channel fishery for common cuttlefish (report).
- Assessing the efficacy of egg receptors within fishing traps used to target common cuttlefish (report).
- Egg survival and maternal investment (report).
- Mitigating cuttlefish egg mortality post fishing activity (poster).
- Supporting sustainable sepia stocks (presentation).

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Introduction

The Common cuttlefish *Sepia officinalis* L. 1758 is a marine mollusc within the class of cephalopoda. The class of cephalopoda can be further separated into two distinct clades; 1) nautiloidea, which includes nautilus, and 2) coleoidea, incorporating the octopodiformes (octopuses and vampire squids) and decapodiformes (cuttlefish and squids). Members of the class cephalopoda can be found in all major marine environments around the world (Reid *et al,* 2005).

Historically, the English Channel population of the common cuttlefish *S. officinalis* was considered a non-target species for commercial fishers with low values and insignificant effort expressed on the stock. This position has dramatically changed in recent years (Dunn 1999). *S. officinalis* now represent an important commercial fishery to many European nations (Bloor, 2012; Bloor, *et al,* 2013a; Keller, *et al*, 2014). The biology and ecology described in this report directly influence this fishing activity. For further information on the fisheries, read the Fishing pressure report.

Biology

Physical description

The common cuttlefish has a large head with relatively large eyes. The front of the head is tipped with eight arms and two tentacles, and these appendages are positioned radially around a forward positioned mouth (Figure 1). The arms have rows of suckers along them, while the tentacles have a number of suckers at their end. The mouth parts are formed of a structure resembling a bird's beak. Directly behind the head is an oval shaped body, fringed with a single fin down each side. The skeletal mass of a cuttlefish is formed of a single internal 'cuttlebone'. The cuttlebone is formed of a porous structure consisting predominantly of aragonite; a type of calcium carbonate. The cuttlebone is important not just for structure, but also functions in maintaining buoyancy (Reid *et al,* 2005).

Common cuttlefish have a relatively short life cycle of between 18 and 24 months. During this time they grow rapidly and can reach a maximum mantle length of 49 cm and weigh up to 4 kg (Dunn, 1999; Gras *et al,* 2014; Gras *et al,* 2016; Reid *et al,* 2005).

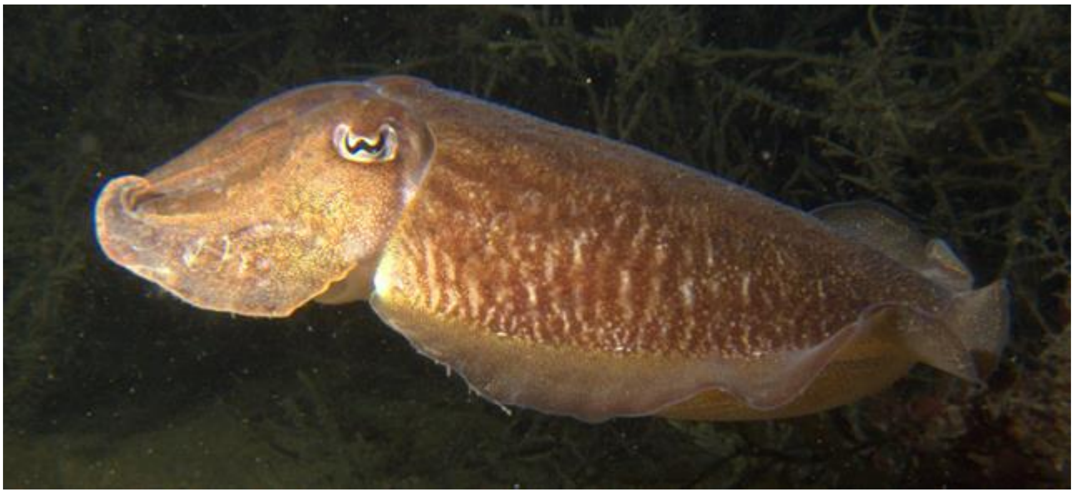

Figure 1. The Common cuttlefish, *Sepia officinalis*. Image credit: © Rik Girdler.

Locomotion and respiration

The main form of propulsion in cuttlefish occurs by pushing water out through its siphon. The siphon is a protruding tube structure that is situated beneath the head at the front of the body. The vertical positioning of cuttlefish is controlled through the transport of gases into and out of the internal cuttlebone, which affects its buoyancy and position within the water column (Bloor *et al,* 2013b). Although the locomotion and respiration musculature systems have been decoupled in cuttlefish, the systems function in a very similar fashion. During both, water is drawn into the mantle cavity, passing over the gills and exits via the siphon. Cuttlefish are very effective at extracting oxygen from the water as it passes counter-current to the blood flow of the gills. The oxygen carrying molecule within the blood of cephalopods is hemocyanin, which gives the blood a distinctive blue-green colouration (Melzner *et al,* 2007).

Vision

The eye of a cuttlefish has a single lens, and a distinctive 'W-shaped' pupil. The visual information gathered by the eye travels along a relatively large optic nerve. The structure of a cuttlefish's eye functions to provide cuttlefish with a high level of visual acuity with strong spatial perception and the ability to distinguish fine details and subtle changes in the contrast of their surroundings. Despite a high level of visual acuity cuttlefish are colour blind The colour changing abilities of a cuttlefish are driven by visual stimuli. From crypsis to startle techniques, cuttlefish visually assess their surroundings before adapting their colouration to suit their requirements. Despite a strong reliance on visual stimuli and a high level of visual acuity, a number a studies have shown that cuttlefish are colour blind (Chiao *et al*, 2005; Chiao *et al*, 2011; Mäthger *et al,* 2006*;* Mäthger *et al,* 2008).

Chromatophores

The colour changing ability of cephalopods is unrivalled in the animal kingdom and cuttlefish are no exception. Their skin contains a range of specialist cells that enable the cuttlefish to rapidly change their colour and patterning. The most important of these cells are pigmented chromatophores, which work in conjunction with reflective iridophores and light scattering leucophores. The chromatophores of cuttlefish have three distinct pigmentations; yellow, orange and dark brown. The dorsal surface of the cuttlefish has all three pigmented chromatophores, the ventral side lacks the dark brown chromatophores (Mäthger *et al,* 2008). Each chromatophore is an elastic sacculus containing pigment which is attached to radial muscles, each with its own neurological connection. Upon contraction of the radial muscle, the saccule expands and moves closer to the surface of the skin (Messenger, 2001).

The ability to change colour has a wide range of applications for the cuttlefish including crypsis, startle techniques to confuse both predators and prey alike as well as signalling and communicating with other cuttlefish (Adamo *et al,* 2006; Buresch *et al,* 2011; Chiao *et al,*2005; Chiao *et al*, 2011, Mäthger *et al,* 2008; Messenger, 2001).

Colour patterns

When avoiding detection, cuttlefish use visual cues from their local environment, particularly the contrast and size of the surrounding substrate to inform the best patterning to avoid detection (Chiao *et al,* 2005). Depending on the local substrate, the cuttlefish will adopt one of four main patterns:

- Dark mottled colouration, with a coarse high contrasting dark and light mottled pattern
- Light mottled colouration, similar to the dark mottled pattern with less contrast between the light and dark areas
- Disruptive, bold dark and light bars both transverse and longitudinal across the mantle
- Stippled pattern, a pale tone with dark stippled marks across the mantle
  (Adamo *et al,* 2006; Buresch *et al,* 2011; Chiao *et al*, 2011; Hanlon and Messenger, 1988).

If crypsis is unsuccessful, the cuttlefish may use anti-predator patterning. The predominant anti-predator pattern is a deimatic pattern; the cuttlefish often flattens its body, whilst adopting a pale tone with two large, dark eye spots appearing near the rear of the mantle (Adamo *et al,* 2006). Other anti-predator patterns include a uniform dark colour often combined with either splayed arms or the two upper arms raised.

During hunting, cuttlefish have often been observed using a pattern known as passing cloud. This pattern is formed of broad light and dark bands of colour moving across the dorsal side of the mantle.

This pattern is often combined with the raising and posturing of the two upper arms. This behaviour is thought to distract or lure the cuttlefish's prey (Adamo *et al,* 2006).

Many studies have been conducted into the conspecific signalling patterns used by *S. officinalis.* The most commonly observed pattern is the intense zebra pattern, and this colouration is used by males to signal their sex to other males, and to attract potential mates. In male-male encounters, the intense zebra pattern may also be combined with a darkening of the facial area, with the more dominant male exhibiting a darker face. If both males have equally dark faces, then the encounter is likely to lead to aggressive physical contact and may result in injury (Hanlon and Adamo, 1996).

Ink sac and funnel organ

As a general rule, all orders of Coleoida (including cuttlefish) have ink sacs and the ability to produce ink, whereas members of Nautiloidea do not. Since the divergence of the two clades, some coleloids have subsequently lost their ink sacs, mostly including deep water or nocturnal shallow water species. In the cephalopods that do produce ink, the ink sac is present at hatching, and this grants new hatchlings the ability to produce and release ink (Derby, 2014).

The ink that cuttlefish secrete is produced within two glandular organs within their bodies. The first of these is the ink sac, which produces a melanin rich black ink. This ink is secreted into the lumen of the ink sac by specialised glands. The ink stored in the ink sac is released via the hindgut and anus under muscular control. The second organ involved in this process is the funnel organ, also known as the organ of verrill. This organ secretes a mucus, rich in free amino acids and ammonium and is located near the siphon (Derby *et al*, 2007).

The combined secretions of both organs make an effective defence mechanism. The melanin rich ink provides an effective visual obstruction that provides cover for the cuttlefish. Whilst the mucus secreted from the funnel organ is high in compounds that excite the chemoreception pathways of many marine predators, this causes the predator to attend to the ink cloud, reducing its interest in the cuttlefish. Both the increased cover and distraction caused by the ink cloud enables the cuttlefish to evade its predators (Derby *et al*, 2007; Derby, 2014).

Reproduction

Common cuttlefish are intermittent terminal spawners; spawning occurs during latter stages of their lives. Females typically stop feeding during this time and undergoes no somatic growth. After laying a number of batches of eggs over a few months, the breeding cuttlefish undergo mass mortality (Bloor *et al,* 2013a; Guerra*,* 2006; Rocha *et al,* 2001).

Mate selection

Mate selection in cuttlefish is a female choice with males competing against one another for copulation and fertilisation opportunities. Females select mates based on assessment of either secondary sexual traits or ornamentation. Although the process is understood, the specific selection criterion for *S. officinalis* has not been clearly defined, some reports have suggested that the sexual dimorphic body patterning of males (zebra patterning) may be involved (Bloor *et al,* 2013a).

Mating

S. officinalis are polyandrous with females collecting and storing the sperm packages of multiple males. The sperm packages of different males are stored within a specialised copulatory pouch beneath the buccal mass. Although the process is unclear, further mate selection is thought to occur post copulation, with females using sperm packages from multiple males to fertilise single batches of eggs (Naud *et al,* 2005).

Before male cuttlefish transfer their spermatophores into the copulation pouch of the female, they will jet strong water currents toward the buccal region of the female in an attempt to flush out the spermatophores of previous couplings. Then, using a specialised organ known as the hectocotylus located on the fourth left arm, the male deposits his spermatophores into the female's copulation pouch. Within the copulation pouch, the spermatophores can remain viable for up to four to five months before being used by the female (Bloor *et al,* 2013a). After copulation, the male will often stay close to the mated female and will attempt to prevent other males from copulating with her (Hanlon *et al,* 1999).

Fertilisation

Fertilisation of *S. officinalis* eggs occurs externally after the secretion of two gelatinous envelopes that form the egg capsule. The mature oocyte passes through the oviducal duct, where it is partially embedded into the first egg capsule. The embedded oocyte is then released into the mantle cavity via the distil oviduct. Within the mantle cavity the nidamental glands release the second, ink stained egg capsule. As the maternal cuttlefish lays the egg, she releases spermatozoa stored within the copulatory pouch around the encapsulated egg. The presence of sperm-attracting peptides in the egg increases the probability of gamete collision and fertilisation (Zatylny *et al,* 2002).

Fecundity

The potential fecundity of common cuttlefish within the Aegean Sea population was reviewed and found to be between 3700 and 8000 eggs in mature pre-spawning animals. The same study calculated the realised fecundity of common cuttlefish from specimens of the same breeding population and found that females (dorsal mantle length 94-247 mm) have both mature and ovulated eggs in numbers between 130 and 839, with a strong correlation between increasing maternal size and increasing numbers of mature eggs (Bloor *et al,* 2013a; Guerra, 2006).

Egg laying

The spatial and temporal variations in oviposition (egg laying) represent maternal choices that can greatly affect offspring fitness and survival. Oviposition timing within the English Channel population is driven by sea temperature, and follows the inshore migration to suitable breeding grounds (Bloor *et al,* 2013a; Dunn, 1999; Guerra, 2006).

The impacts of oviposition timing are less important than those of site selection for the fitness of the maternal cuttlefish, as a single female cuttlefish may lay multiple batches of eggs over a protracted period of time throughout the breeding season (Rocha *et al,* 2001). Oviposition site selection can have a massive impact on the survival of young cuttlefish; with a poor decision potentially leading to increased rates of predation, sub-optimum environmental conditions and reduced prey availability (Bloor *et al,* 2013a).

Common cuttlefish lay their eggs in clusters and predominantly in shallow water often less than 40 metres deep. The eggs are attached to structures that are fixed to the seabed and these structures may be either natural or anthropogenic. Naturally occurring structures that have had cuttlefish eggs laid on them include plants and macroalgae such as seagrass (*Zostera marina)* and serrated wrack (*Fucus serratus*). Sessile animals can also function as oviposition sites, such as sponges (*Porifera* sp.) and the peacock worm (*Sabella pavonina*) a polychaete tube worm. Cuttlefish have even been known to lay their eggs on mobile animals (Bloor, 2012; Bloor *et al,* 2013a; Guerra, 2006; Guerra *et al,* 2016). Anthropogenic structures that have been recorded as egg laying sites for cuttlefish include fishing gear such as nets, traps/pots and ropes including mooring and anchor lines (Blanc and Daguzan, 1998; Bloor, 2012; Bloor *et al,* 2013a; Melli *et al,* 2014, Sasikumara *et al,* 2015).

In 2016, Guerra *et al* reviewed the habitat preference of egg laying cuttlefish of the Cíes Islands (NW Spain). This study showed that common cuttlefish preferred habitats with hard substrates containing structural fauna such as seafans and tube worms (Guerra *et al,* 2016). In contrast, additional studies have identified habitats with soft substrates such as sand as preferred oviposition sites (Bloor, 2012; Bloor *et al,* 2013a). The presence of cuttlefish eggs has a strong positive effect on a maternal cuttlefish's decision when choosing a potential oviposition site (Blanc and Daguzan, 1998).

Gestation period

The gestation period for cuttlefish ranges between one and three months, and is highly dependent on water temperature, with increasing temperatures reducing gestation time (Bloor *et al,* 2013a; Guerra*,* 2006; Martins *et al,* 2017). At 20°C, cuttlefish eggs will hatch at between 40-45 days, while eggs maintained at 15°C require 80-90 days to hatch (Bloor *et al,* 2013a).

An elevated temperature during gestation has other implications on the developing embryo. In 1991 Bouchard found that eggs incubated at 15°C produced cuttlefish nearly twice the size of eggs incubated at 24°C (Bouchaud, 1991). As the eggs came from the same maternal source, the difference in size at hatching was attributed to the warmer temperatures affecting the metabolism of embryos, reducing the amount of energy available for embryonic growth (Bloor *et al,* 2013a; Bouchaud, 1991).

Hatching

During the later stages of embryonic development, the egg swells, causing the ink stained membrane to be stretched and become more permeable to light. This allows the cuttlefish to form a diurnal cycle and to time its hatching a few hours after dusk to reduce the risk of predation (Bloor, 2016). The cuttlefish is also able to receive visual cues informing the abundance of different prey (Darmaillacq *et al,* 2008; Guibé *et al,* 2012). Newly hatched cuttlefish can survive on their yolk reserves for up to three days after hatching, but they are able to hunt and consume prey within hours of hatching (Blanc *et al,* 1998; Guerra, 2006).

Within the English Channel population, cuttlefish hatch at between 6 and 9 mm (mantle length). The young cuttlefish are very similar to the adults in both behaviour and morphology (Bloor *et al,* 2013a; Guerra*,* 2006).

Ecology

Hunting behaviour

Three distinct phases are observed during cuttlefish hunting behaviour; attention, positioning, and seizure.

During attention and positioning, the cuttlefish notices its prey and approaches, moving until it is aligned with its prey approximately one mantle length distant. These phases are often accompanied with changing body patterns and the two upper arms are raised.

During the final phase (seizure), the cuttlefish uses one of two different manoeuvres. The first, a tentacle strike is predominantly used against faster moving prey; two tentacles are rapidly extended to grab the prey. The second seizure manoeuvre, an arm-grab, involves the cuttlefish pouncing on its prey and wrapping its arms around it (Adamo *et al,* 2006).

After seizing its prey the cuttlefish quickly bites and its venomous saliva, containing cephalotoxins produced in the two posterior salivary glands, causes paralysis (Cornet *et at,* 2014).

Adult diet

The diet of adult cuttlefish incorporates a wide range of different organisms and includes crustaceans, molluscs, polychaete worms and bony fish. Crustaceans, such as mysids, shrimps, prawns and crabs are often the preferred prey of cuttlefish. Sandeels and gobies made up the most common groups of fish eaten by cuttlefish. The most abundant molluscs in the diet of *S. officinalis* are sepiolids and sepiids (squids). Cuttlefish will frequently exhibit cannibalistic tendencies and larger individuals will attack and consume smaller members of the same and closely related species (Blanc *et al,* 1998; Bloor*,* 2012; Guerra 2006).

Juvenile diet

The diet of juvenile cuttlefish incorporates a high percentage of small crustaceans. One study examined the stomach contents of over 600 individuals, with a dorsal mantle length of less than 85 mm, and showed that 89% of the stomach contents were small crustaceans (Blanc *et al,* 1998). A number of other studies have also reported a strong preference for small crustaceans within the diet of *S. officinalis* (Bloor *et al,* 2013a; Darmaillacq, *et al,* 2008; Guerra 2006; Guibé *et al,* 2012; Neves *et al,* 2009; Pinczon du Sel *et al,* 2000).

Juvenile cuttlefish are able to imprint food preferences during the last stages of development within their egg capsule, and this process continues during the first few hours following their hatching. This allows the cuttlefish to be able to select suitable prey items that are abundant within the local environment (Darmaillacq *et al,* 2008; Guibé *et al,* 2012).

The shift in the diet of cuttlefish from small crustaceans as juveniles to larger crustaceans and fishes when adult represents a common behavioural trait employed by many marine organisms. The changing diet between age classes reduces the incidence of intraspecific competition (Neves *et al,* 2009).

Trophic level

Stable isotope analysis of nitrogen within the amino acids of both the mantle and cuttlebone of cuttlefish allowed the calculation of a trophic level of 3.6 for adult cuttlefish (Ohkouchi, *et al,* 2013). The results published in 2013 by Ohkouchi *et al* were higher than the results of a previous study which identified common cuttlefish as one of the apex predators within the sampled area with a trophic level of 2.4 (Vinagre *et al,* 2012). However, both studies indicated that the relatively low trophic level of *S. officinalis* is due to their reliance on benthic crustaceans for a large proportion of their diet (Ohkouchi *et al,* 2013; Vinagre *et al,* 2012).

Predation of eggs

Both fish and invertebrates have been known to consume the eggs of cuttlefish. Small fish such as tompot blennies (*Parablennius gattorugine)* were observed predating on cuttlefish eggs during the later stages of their development (Guerra and González, 2011). Decapods such as the European lobster (*Homarus gammarus*), the edible crab (*Cancer pagurus*), molluscs including the purple dye murex (*Bolinus brandaris),* echinoderms such as the melon sea urchin (*Echinus melo)* and the purple sea urchin (*paracentrotus lividus*) were all recorded preying on cuttlefish eggs (Martins *et al,* 2017). During conversations with fishers operating within the demersal trammel net fishery of Hastings, England, a number of active fishers reported large amounts of cuttlefish eggs in the stomachs of cod (*Gadus morhua*) and occasionally Dover sole (*Solea solea*) (Joy *pers comm* 2018; Coglan *pers comm* 2018).

Predation of juveniles

As juveniles, common cuttlefish are predated on by many species. During a study conducted in the cuttlefish spawning grounds of Morbihan Bay (south Brittany, France), the stomach contents of 28 species were studied, five of which were found to have juvenile cuttlefish within their stomachs. These included the grey triggerfish (*Balistes carolinensis*), the European bass (*Dicentrarchus labrax*), the ballan wrasse (*Labrus bergylta*), the lesser spotted dogfish (*Spondyliosoma cantharus*) and the conger eel (*Conger conger*). The size of cuttlefish consumed by these predators ranged from between 8 to 61 mm dorsal mantle length and represented cuttlefish between 0 and 4 months of age (Blanc and Daguzan, 1999). Cuttlefish are cannibalistic and an important predator of young cuttlefish are older cohorts, which will frequently predate on newly hatched juveniles (Blanc *et al,* 1998; Bloor*,* 2012; Guerra 2006).

Predation of adults

Adult cuttlefish are often predated on by the apex predators of their respective food webs. The predators of adult cuttlefish are represented by many diverse taxa, including marine mammals such as risso's dolphins (*Grampus griseus*) and monk seals (*Monachus monachus*), large fishes such as the European bass (*D. labrax*) and Atlantic cod (*G.* morhua), as well as elasmobranchs including the smoothhound shark (*Mustelus mustelus*) and greater spotted dogfish (*Scyliorhinus stellaris*) (Guerra, 2006; Langridge, 2009; Vinagre *et al,* 2012).

Predator avoidance

Common cuttlefish are predated on at every stage of their life cycle. They apply a number of predator avoidance techniques and can vary these depending on the type of predator.

The primary defence mechanism is crypsis, which involves the cuttlefish either burrowing into the substrate or changing its colour and patterning to blend in with its surroundings (Adamo *et al,* 2006; Buresch *et al,* 2011; Chiao *et al,*2005; Chiao *et al*, 2011, Mäthger *et al,*2008; Staudinger *et al,* 2013). This technique is frequently applied against visually stimulated predators such as large teleost fish species (Langridge, 2009; Staudinger *et al,* 2013). If the cuttlefish is detected, it then can rapidly change its patterning in an attempt to startle its predator.

For persistent predators or those that rely more heavily on chemoreception such as elasmobranchs, the cuttlefish can squirt a disorienting cloud of ink whilst rapidly retreating (Derby *et al,* 2007; Derby, 2014; Staudinger *et al,* 2013).

Habitat preference

Cuttlefish are a benthic species that lives in close association to the seabed. Cuttlefish generally prefer softer substrates such as sand or mud, although they can also be found over rocky substrates (Bloor, 2012; Bloor *et al,* 2013a Bloor *et al,* 2013b; Guerra*,* 2006; Keller, *et al*, 2014).

Geographical range

The natural range of common cuttlefish stretches throughout the north eastern waters of the Atlantic Ocean on the continental shelves, from southern Norway and northern England, south to the coasts of Senegal. They also occur throughout the Mediterranean Sea (Guerra, 2006; Reid *et al,* 2005).

The northern and southern boundaries of their range are likely to be governed by their thermal tolerance, with the northern limit set by a temperature of 10°C. Common cuttlefish will not survive a prolonged exposure of temperatures below 10°C; at this temperature they stop feeding and if the temperature does not rise above 10°C, they will eventually expire (Domingues *et al,* 2002). The use of both laboratory experimentation and natural observation has suggested that the upper temperature limit for cuttlefish is 30°C, and this temperature sets the southern limits of the distribution (Domingues *et al,* 2001; Guerra*,* 2006).

Depth range

They are found at depths ranging between 1-2m down to 200m, although they are far more common above 100m (Guerra*,* 2006). Work by Ward and Boletzky in the 1980's suggests that that cuttlefish cannot inhabit water deeper than 200m, due to the pressure on the internal shell of the cuttlefish and that at such depths the cuttlefish shell may implode (Ward and Boletzky, 1984).

Salinity tolerance

Cuttlefish can tolerate a variety of salinities and can be found in the brackish waters of coastal lagoons with individuals being observed at a salinity of 27 PSU (Guerra, 2006; Reid *et al,* 2005). A trend can be seen between the age and mantle length of cuttlefish*,* and their tolerance of lower salinities. A decrease in salinity often correlates with a reduction in the average age. This is due to younger specimens having a greater ecophysiological plasticity, allowing them to colonise regions of the lagoon system unavailable to larger individuals which reduces cannibalism and intraspecific competition (Reid *et al,* 2005).

A study conducted on the embryonic development of cuttlefish showed that elevated salinities up to 37±3 PSU has little impact on the development and hatching rates of embryonic *S. officinalis* (Domingues et al, 2001; Guerra*,* 2006). However, reductions in salinity can have a greater effect on the embryonic development of cuttlefish (Bloor *et al,* 2013a; Guerra, 2006)*.* Paulij *et al* collected cuttlefish eggs from the wild and held them under a variety of physical parameters, and showed that development and hatching occurred at 26.5 PSU, although reductions in both development and hatching rates were shown at salinities below 28.7 PSU. The same study showed that at salinities below 23.9 PSU no hatching occurred, and that at salinities below 22.4 PSU the embryos became extremely malformed (Paulij *et al,* 1990). The deformities produced by reduced salinities are likely to be caused by the increased energy demand of the embryos when exposed to increased osmotic stress (Bloor *et al,* 2013a). The optimum salinity for *S. officinalis* embryonic development and hatching rates is between 29.8 and 34.0 PSU (Bloor *et al,* 2013a).

Migration

Many studies have reviewed the annual migration of the English Channel common cuttlefish from the offshore over wintering habitat to the inshore breeding grounds*.* This migration pattern is supported by fisheries' capture data from which spatio-temporal shifts in the distribution and abundance of cuttlefish can be observed (Dunn, 1999; Wang *et al*, 2003).

During early spring, adult cuttlefish begin to move towards their inshore breeding grounds. One of the main triggers for this migration is believed to be sea temperature (Wang *et al,* 2003). The breeding season extends from April to July and during this time the distribution of cuttlefish is concentrated in the inshore coastal waters on both sides of the English Channel (Bloor *et al,* 2013a; Bloor *et al,* 2013b; Wang *et al,* 2003).

In the early autumn, the nonbreeding adults and newly hatched offspring begin to move toward the western regions of the English Channel. Between October and November, the majority of cuttlefish move offshore and aggregate in their overwintering grounds. These grounds are centred around a region of the middle western English Channel known as the Hurd Deep. The main reason this region is a suitable over wintering ground for cuttlefish is its depth of water, combined with prevailing Atlantic currents which ensure that the seabed temperature rarely falls below 10°C (Bloor *et al,* 2013a; Bloor *et al,* 2013b; Domingues *et al,* 2002; Wang *et al,* 2003).

Conclusion

The ability to change colour combined with high visual acuity, prehensile arms and venomous saliva enables cuttlefish to be highly effective predators. As such cuttlefish often occupy high positions within their respective food webs (Adamo *et al,* 2006). However, cuttlefish are predated on by a range of commercially important species such as the Atlantic cod (*Gadus morhua*).

The rapid rate of maturation and short life span of common cuttlefish creates a short generation time. This enables the cuttlefish to maximise their intrinsic rate of population growth despite their relatively low individual fecundity. The maximising of their intrinsic population growth, affords the cuttlefish some protection against the impacts of fishery exploitation. However this life history strategy is highly dependent on a minimum number of offspring being produced ever year and therefore they can be susceptible to rapid depletion by fishing pressure. As such, cuttlefish should be managed to maintain a critical minimum spawning biomass. This implies that as a population approaches a minimum spawning biomass, that fishing should cease (King and McFarlane 2003).

The seasonal migrations and resulting aggregations of common cuttlefish, are driven by both the temperature tolerance of cuttlefish and their breeding strategy. Unfortunately, these aggregates allow for high levels of exploitation with relatively low levels of fishing effort.

Because all cuttlefish reproduction occurs at the end of their life cycle, almost all fisheries target cuttlefish before they have had chance to reproduce. One exception to this is the inshore pot and trap fisheries. These fisheries target cuttlefish at the end of their lives, during their breeding season. This will often result in the cuttlefish having the opportunity to lay some eggs before being caught. The traps and pots used to target cuttlefish are frequently the last sites of egg laying for the captured cuttlefish. If these eggs can be easily removed from the cuttlefish traps and pots and quickly returned to sea, this will further reduce the ecological impact of the cuttlefish trap and pot fishery. For further information on this, read the other reports from this project.

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