



MarLIN

Marine Information Network

Information on the species and habitats around the coasts and sea of the British Isles

Common cuttlefish (*Sepia officinalis*)

MarLIN – Marine Life Information Network
Marine Evidence-based Sensitivity Assessment (MarESA) Review

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Two individuals hovering over the sea bed.
 Photographer: David Nicholson
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See online review for
 distribution map

Distribution data supplied by the Ocean Biogeographic Information System (OBIS). To interrogate UK data visit the NBN Atlas.

Researched by	Eliza Gibson-Hall & Emily Wilson	Refereed by	This information is not refereed.
Authority	Linnaeus, 1758		
Other common names	-	Synonyms	-

Summary

🔍 Description

The common cuttlefish *Sepia officinalis* is a relatively broad and somewhat flattened cephalopod, appearing oval in cross section. It has a mantle length of up to 45 cm. Paired fins run from behind the head to the tip of the body. *Sepia officinalis* has eight arms and two elongated tentacles. These arms are specialised for grasping prey after it has been seized by the tentacles. The tentacles are cylindrical, muscular structures which can be quickly elongated. They end in a tentacular club, with five to six rows of suckers, that is specially adapted for prey capture. Males have adapted one of the arms for the purpose of transporting sperm into the female's buccal cavity, located in her mouth. Individuals are capable of very rapid colour change, especially when threatened. They may also take the colour or patterning of its background.

📍 Recorded distribution in Britain and Ireland

Recorded along the south coast and west coast of England and Wales and around the Channel Islands and the Isle of Man. Sporadic records exist along the east coast of Britain and the west to the north coast of Scotland, including the Hebrides. Some records from the north-east and south-west of Ireland.

Global distribution

Recorded from the eastern Atlantic; from the Baltic and North Sea to South Africa and in the Mediterranean.

Habitat

Found on sandy and muddy substrata, in the shallow sublittoral and offshore to 200 m, but typically to 100 m depth. It is a demersal species and prefers moderately warm, shallow coastal waters as well as continental shelves.

Depth range

0-200 m

Identifying features

- They have eight arms and two tentacles which both end in a tentacular club with 5-6 rows of suckers.
- Cuttlebone anteriorly and posteriorly rounded, with parallel sides.
- Colour - very variable; may be black-brown, striped or mottled on the dorsal surface, paler to white on the ventral surface.

Additional information

Males are larger than females, and slightly more frequent (Dunn, 1999). *Sepia elegans* is smaller, has two rows of suckers on arms and has an acute lobe on its dorsal mantle margin. *Sepia officinalis* has been observed to undergo a 'sleep-like state'. Observed behaviour included a quiescent state, changes in body colouration, twitching of arms, and rapid eye movement, which could be an indication of REM sleep (Frank *et al.*, 2012). This state occurs periodically during periods of inactivity and can last on average 135 seconds (Frank *et al.*, 2012). Cuttlefish is also said to have one of the largest brain-to-body ratios of any invertebrate.

Listed by



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Biology review

☰ Taxonomy

Phylum	Mollusca	Snails, slugs, mussels, cockles, clams & squid
Class	Cephalopoda	Cuttlefish, nautilus, octopus & squid
Order	Sepiida	Cuttlefish
Family	Sepiidae	
Genus	Sepia	
Authority	Linnaeus, 1758	
Recent Synonyms	-	

🌿 Biology

Typical abundance	Moderate density
Male size range	8-45 cm
Male size at maturity	14-24 cm
Female size range	12-29 cm
Female size at maturity	15-22 cm
Growth form	No information
Growth rate	1.4-3.3cm/month
Body flexibility	Low (10-45 degrees)
Mobility	Swimmer
Characteristic feeding method	Predator
Diet/food source	Heterotroph
Typically feeds on	Brachyuran crabs and demersal fish (gobiids and syngnathids), with minor amounts of amphipods and little cannibalism.
Sociability	Solitary
Environmental position	Demersal
Dependency	Independent.
Supports	Host <i>Doridicola longicauda</i> (Claus 1860)
Is the species harmful?	Yes Saliva contains cephalotoxin which induces paralysis and immobilizes prey.

🏛️ Biology information

Size

Size is measured as dorsal mantle length. The sizes of breeding individuals range from 8 to 45 cm in males and from 12 to 29 cm in females (Goff & Daguzan, 1991). The largest individual to be recorded reached 60 cm in length (Compton & Wiley, 2011). Due to a variation in size amongst individuals, juveniles are usually defined as non-mature adults (Guerra, 2006) (see size at maturity).

Growth

The growth rate of juveniles is generally faster than adults. In juveniles, growth rates also depend on the month of hatching. Juveniles hatched in early summer, June, had a growth rate of around 1.2 mm/day. In comparison, juveniles born in late summer, August, had a reduced growth rate of around 0.5 mm/day. This is thought to be due to a difference in water temperature during embryonic development and post-hatching (Challier *et al.*, 2002). Nutrition and the availability of food is also important for the initial growth rate of juveniles. Cultured juveniles that were starved during the first twenty days of rearing displayed a negative growth rate and ultimately died (Koueta & Boucaud-Camou, 2001).

Adults have a more linear growth rate (Challier *et al.*, 2005) that almost ceases during winter migration to colder offshore waters (Dunn, 1999). The growth rate of *Sepia officinalis* decreases continuously with an increase in size (Domingues *et al.*, 2001). A maximum lifespan of two years is common with an exception of some individuals reaching four years of age in culture (Bettencourt & Guerra, 1999). In areas of higher temperatures, such as the Portuguese coast, the time taken to reach sexual maturity is far less compared to English, colder, waters. This results in a reduced lifespan of one year (Gras *et al.*, 2016).

Camouflage ability

One of the primary defence mechanisms against potential predators is to camouflage and stay hidden. *Sepia officinalis*, amongst other cephalopod species, are able to undergo countershading. This behaviour means that if an individual is rotated 90 degrees their chromatophores expand and contract accordingly to make sure the underside of the body is now the colour of the upper half and vice versa. This allows the cuttlefish to remain camouflaged and prevents it from being conspicuous (Ferguson *et al.*, 1994). Cuttlefish are able to scale the intensity of their body patterning depending on the light intensity surrounding them. This is thought to allow them to conserve energy (Buresch *et al.*, 2015). In extremely low light conditions *Sepia officinalis* do not appear to camouflage to the substratum (Buresch *et al.*, 2015).

Mobility and sociability

Sepia officinalis is a mobile species. Buoyancy is maintained by the species' cuttlebone. The internal cuttlebone is incredibly porous and is used by the species to adjust buoyancy by increasing and decreasing liquid flow into the bone (Hastie *et al.*, 2009).

Sepia officinalis are not very sociable and do not form shoals in the wild. In culture, they will tolerate each other unless they are under periods of extreme food deprivation (Guerra, 2006). Juveniles tend to show a high tolerance for other individuals compared to adults. After four months post-hatching a feeding hierarchy is clearly visible in culture (Hanlon & Messenger, 1996).



Habitat preferences

Physiographic preferences	Estuary, Open coast, Ria / Voe, Sea loch / Sea lough
Biological zone preferences	Lower circalittoral, Lower infralittoral, Sublittoral fringe, Upper circalittoral, Upper infralittoral
Substratum / habitat preferences	Coarse clean sand, Fine clean sand, Mud, Muddy sand, Sandy mud
Tidal strength preferences	No information
Wave exposure preferences	No information
Salinity preferences	Variable (18-40 psu)
Depth range	0-200 m

Other preferences	No text entered
Migration Pattern	Seasonal (environment), Seasonal (reproduction)

Habitat Information

The common cuttlefish occurs in both warm and temperate environments and migrates to and from each environment depending on the stage in the life cycle (Boletzky, 1983). They occur predominantly on sandy-muddy bottoms from the coastline to approximately 200 m. The most common occurrence is at 100 m. Below 200 m the ambient pressure of the water is enough to implode the inner shell (Ward & Boletzky, 1984). The shells of newly hatched individuals can implode between 50 and 100 m meaning hatchlings are found in shallow, coastal waters (Guerra, 2006).

Juveniles occur in coastal habitats with a preference for sandy substratum (for hiding) and seagrass beds. Seagrass beds are highly productive areas and serve as a protective environment providing shelter for juveniles (Jackson *et al.*, 2001). Seagrass also reduces currents and promotes sediment deposition providing the correct environment for juveniles (Camou, 2001). In the central Cíes islands, egg abundance was highest in the most sheltered zones in depths of 8-13 m (Guerra & Castro, 1998; Guerra *et al.*, 2016b).

Habitat expansion

Sepia officinalis is the most northerly-distributed cuttlefish. Models of climate change have predicted that the species may be able to expand its range up to the warming arctic waters. Temperatures would need to be above 7°C as lower temperatures reduce the metabolic processes of the species (Xavier *et al.*, 2016). If *Sepia officinalis* were able to reach into the Arctic Circle and down into the western Atlantic it could reach the east coast of America by 2300 (Xavier *et al.*, 2016). The short maturity time and the constant cycle of generations mean that cephalopods, compared to other groups, are able to adjust faster to a change in environmental conditions (Xavier *et al.*, 2016). Finally, if the species is able to reach Iceland, Greenland or the Faroe Islands they will find seagrass beds and/or kelp that are a perfect habitat for spawning (Xavier *et al.*, 2016).

Life history

Adult characteristics

Reproductive type	Gonochoristic (dioecious)
Reproductive frequency	Semelparous / monotelic
Fecundity (number of eggs)	100-1,000
Generation time	1-2 years
Age at maturity	13-16 months
Season	March - July
Life span	1-2 years

Larval characteristics

Larval/propagule type	Not relevant
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Larval/juvenile development	See additional information
Duration of larval stage	Not relevant
Larval dispersal potential	No information
Larval settlement period	Not relevant

Life history information

Lifespan

If food availability is restricted in early life this may result in delayed maturation and an extended lifespan (Boletzky, 1974). Mortality in females occurs after spawning, which can take several weeks to a few months (Guerra, 2006). Biannual life cycles have been observed frequently. In the English Channel, hatchlings born from July to September grew rapidly. The juveniles migrate from the inshore nursery grounds to overwintering in deeper waters. They return inshore as soon as they exhibit the first signs of sexual maturity (Guerra, 2006).

Size at maturity

Maturity in males usually occurs by September at around thirteen months old (Guerra, 2006). Maturity is based on observation of both testicle size and the position of spermatophores (Gras *et al.*, 2016). Female maturation begins slightly later and tends to take longer (Guerra, 2006). Maturity in females is characterized by the size of the oocyte and the development of the nidamental glands (Gras *et al.*, 2016). There appears to be an annual variation in the size at sexual maturity. In 2011, the size at which sexual maturity was reached for both sexes, in the English Channel, was lower than in 2010. For example, sexually mature males were 14 cm in 2011 compared to 16 cm in 2010 (Gras *et al.*, 2016). There is also a variation between group I breeders and group II breeders. Group I breeders, which spawn during the first year of life, reach sexual maturity at around 14.5 cm (14 cm males, 15 cm females). However, Group II breeders, reproduce during their second year of life and are able to grow for longer and reach maturity at ca 23 cm (24 cm males, 22 cm females) (Gauvrit *et al.*, 1997).

Temperature also appears to affect the age at which juveniles reach sexual maturity. Individuals reared at 20°C became sexually mature at seven months and were 14 cm in length. In contrast, those raised in 10°C remained immature at seven months and measured only 5 cm long (Richard, 1996 as cited in Bloor *et al.*, 2013).

Fecundity

In the English channel, females lay, on average, only 200-550 eggs depending on the size of the female (Boletzky, 1987). The potential fecundity of sexually mature females in the Aegean Sea is 3,700 to 8,000 oocytes (Laptikhovsky *et al.*, 2003). Despite this potential, the average number of eggs released from spawning females was 1000-3000 prior to death (Bloor *et al.*, 2013) in the English Channel. It has therefore been suggested that *Sepia officinalis* females release an equivalent of 50% of their potential fecundity.

In culture, fecundity decreased with each generation resulting in the 7th generation being almost infertile. Forsythe *et al.* (1994) suggested that this could be due to the cultures having a longer lifespan and, therefore, putting more energy into growth rather than reproduction.

Bacteria also play an important role in the reproductive cycle. Symbiotic bacteria are responsible for the colour change in the accessory nidamental glands. This colour change from white to a bright red/orange signifies reproductive readiness. This is thought to play a role in mating and could also

impact the production of fertile eggs (Forsythe *et al.*, 1994). In the same culture, Forsythe *et al.* (1994) observed a lack of pigmentation on the gonads as well as a series of gonad infections. The lack of important bacteria in the culture could also have an impact on the fertility of individuals.

Migration

Inshore migration is governed by reproduction with individuals travelling from several to hundreds of nautical miles (Mangold, 1966). Migration for spawning occurs when an individual reaches maturity (Rodhouse & Nigmatullin, 1996). Mature males and large females of *Sepia officinalis* are the first to migrate inshore to spawning grounds in March and April with spawning occurring from March to July. Migratory patterns have been observed in the English Channel, mostly by fisheries' landing data (Bloor *et al.*, 2013). Hatchlings then emerge during the summer period and undergo rapid growth before beginning their autumn migration offshore to overwintering grounds in the deep central waters (Bloor *et al.*, 2013). The purpose of migrating back inshore to spawn is due to a preferred habitat for eggs and juveniles (Bloor *et al.*, 2013).

In the English Channel, offshore migration occurs in winter and is influenced primarily by a reduction in water temperature as well as the reduction in daylight hours (Guerra, 2006). After spawning occurs adults return back into deeper, offshore areas around October in the UK (Dunn, 1999, Royer *et al.*, 2006). The total distance migrated in each season may exceed 100 km (Du Sel & Daguzan, 1997). Sexually mature individuals do not migrate immediately to an area. Some tagged individuals have been observed to travel 23-35 km along the coast during spawning in 14 days (Bloor *et al.*, 2013b).

Mating

Mating occurs in deeper water. Mate choice occurs in female *Sepia officinalis* and appears to be a preference, not for dominance, but for the absence of zebra banding. This might be because zebra banding infers aggression in the male (Boal, 1997). Males carry up to 1400 spermatophores and females 150-4000 eggs depending on their size. Spermatophores are placed in the female's buccal membrane located above the mouth (Guerra, 2006). A single pair can mate several times and males have been observed to guard their mate post-insemination (Hanlon *et al.*, 1999).

Females are polyandrous and can accept and store sperm from multiple males, and can control which sperm to fertilize her eggs (Naud *et al.*, 2005). This is referred to as the 'cryptic female choice hypothesis' (Eberhard, 1996). More food was consumed by sexually mature females than non-sexually mature females and mature males suggesting a higher demand (Castro & Guerra, 1999).

Spawning

The mantle of female *Sepia officinalis* increases by approximately 10% during the first months of spawning. Females are 'intermittent terminal spawners' as they lay eggs in separate batches (Rocha *et al.*, 2001). For many females, the first phase of laying is slow and linear, ending in an exponential phase of vast egg laying (Boletzky, 1987).

Spawning occurs in shallow water (see sexual migration) and peaks at water temperatures of 13-15°C (Guerra, 2006). In the English Channel, the spawning season extends from February to July but in warmer summers has been observed in August (Dunn, 1999, Wang *et al.*, 2003). Therefore, temperature is thought to be the main regulating factor on the length of spawning (Goff and Daguzan, 1991). If water temperatures remain above 10°C during winter, spawning can occur year-round e.g. in the Ria de Vigo (Guerra & Castro, 1998; Bloor *et al.*, 2013).

Eggs are rarely laid at depths greater than 30-40 m (Boletzky, 1983). The eggs are attached in

grape-like clusters to various seaweeds, seagrass, and sessile animals such as tubeworms or dead structures (Bloor *et al.*, 2013). Eggs can also be attached to previously laid cuttlefish eggs. Attaching eggs to seaweed and seagrass can elevate the eggs and reduce the risk of predation. If conditions are not 'suitable', females can choose how many eggs are laid to reduce mortality of all her offspring (Bloor *et al.*, 2013).

In Morbihan Bay, south Brittany, 18 – 40 million *Sepia officinalis* eggs are laid on cuttletraps from March to September. These traps are emptied every two days by the fishermen but are then stacked on pontoons until further use. This results in mortality of many of the eggs due to their damage and removal from the water (Blanc & Daguzan, 1998).

Embryonic development

Eggs are flask-shaped, coated in ink from the mother and approximately 3-4 cm in length (Boletzky, 1983). As well as acting as a protective barrier, the egg capsule can also protect against environmental stress and microbial infection (Catarina *et al.*, 2017). Bacteria also live inside the egg and provide antifouling and antimicrobial properties alongside a yolk supplying nutrients. *Sepia officinalis* eggs are one of the largest amongst cephalopods (Challier *et al.*, 2005).

Egg development can last from 1 to 5 months depending on the water temperature (Catarina *et al.*, 2017). At 12°C development took 5 months in culture with development ceasing at temperatures below 9°C. However, once temperatures were increased embryogenesis restarted (Bouchaud & Daguzan, 1990, Challier *et al.*, 2004). Eggs cultured at 15°C appeared to use 41% of the egg-yolk for growth and 10% for respiration and excretion. Eggs cultured at 24°C, however, used only 15% of the egg-yolk for growth and used 52% for respiration and excretion. Therefore, *Sepia officinalis* hatched at 24°C were almost half the size of hatchlings grown in 15°C. All the eggs were from the same mother and were around the same size of 23 cm (Bouchaud, 1991). The optimal temperature for embryonic development is 15-18°C (Bouchaud, 1991). Maternal health and nutritional history are also known to influence the size and success of offspring (Steer *et al.*, 2004, cited in Bloor *et al.*, 2013).

Catarina *et al.* (2017) reported that *Sepia officinalis*' eggs are predated by; "the snail *Bolinus brandaris*, the crab *Cancer pagurus*, the hermit crab *Dardanus arrosor*, the lobster *Homarus gammarus*, the invasive blue crab *Callinectes sapidus*, the shrimp *Squilla mantis*, the sea urchins *Echinus melo*, *Cidaris* sp. and *Paracentrotus lividus*, and the starfish *Astropecten aranciacus*".

The egg capsules become thinner and lose their ink making them more transparent towards the end of embryonic development. In this last stage, the eggs are most vulnerable to predation (Catarina *et al.*, 2017). Oxygen also becomes limiting towards the end of embryonic development as both oxygen consumption and ammonia production are at their highest within the egg capsule (Lesser, 2010).

Hatching

In the English Channel, hatching is usually the highest in July and August but may begin as early as May (Challier *et al.*, 2002). The hatchlings are similar to adults in morphology and basic behaviour but only 7-8 mm in length (Boletzky, 1983). No parental care has been observed. Hatchlings are developed enough to actively feed within hours of hatching. They have the ability to adapt if food supply is limited by reducing their growth rate (Boletzky, 1983). Juveniles will stay in breeding grounds until 60 - 120 days old, whereupon they join adults in offshore, winter grounds, (Blanc & Daguzan, 1999, Challier *et al.*, 2002).

The newly hatched cuttlefish will survive off of the inner yolk reserve from the egg for up to the first 305 days or until the reserve 'runs out' (Blanc *et al.*, 1998). The first ten days post-hatching are the most vulnerable for the hatchlings and is the period of highest mortality (Bloor *et al.*, 2013).

Hatchlings show an immediate behavioural response to visual or odour cues. This is thought to suggest that embryos can detect stimuli during development, before hatching (Romagny *et al.*, 2012). Hatchlings also show a habituation to certain repeated visual stimuli (O'Brien *et al.*, 2017).

Embryos hatched in culture undertake sand digging during the first six days. This is presumed to be the initial and preferred predator response for small, newly hatched, *Sepia officinalis*. In order to bury in the sand, the cuttlefish squirts a series of jets of water from a ventral funnel, allowing it to 'wiggle' into the sand. (Boletzky, 1987; Mather, 1986 as cited in Poirier *et al.*, 2004).

Juveniles

Juveniles are able to produce a uniform body pattern during the first few months post-hatching (O'Brien *et al.*, 2017) and are able to detect water movements which are key anti-predatory behaviours. In juveniles, 30-60% of food intake is estimated to be used for growth (Koueta & Bouchaud, 2001). Juveniles are able to catch shrimps with ease in complete darkness suggesting adapted ability to detect prey (Blanc *et al.*, 1998). In the English Channel, they begin to migrate to deeper water in late August (Wang *et al.*, 2003). After migrating back to the in-shore spawning grounds in spring many juveniles will show some signs of sexual maturity. However, they will usually not be fully mature until 13 months old for males and 14-16 for females (Dunn, 1999).

In south Brittany, juveniles born in mid-March to June may become sexually mature as early as November (males) or December (females). This is again thought to be due to the higher temperatures, decreasing the time taken to develop and resulting in a life cycle of only one year (Gauvrit *et al.*, 1998). Most individuals spawn after their second migration offshore-inshore and are known as the second group of breeders. These individuals are larger as they have had longer to grow before reaching sexual maturity (Gauvrit *et al.*, 1998). Although mortality usually occurs post-reproduction in the second-year breeders, some individuals have been reported to even live to three years old (Mattacola *et al.*, 1984).

Population dynamics

Sepia officinalis contributes to around 5-10% of landings to local fisheries in the Mediterranean Sea (Salman *et al.*, 1997, Turan & Yalioglu, 2010). *Sepia officinalis* stocks are comprised of two overlapping annual cohorts of migrating adults and newly hatched juveniles. The English Channel stock has a very high recruitment of 44 – 79 million, which is higher than many other fished cephalopods in the region (Royer *et al.*, 2006). Landing data has shown that older animals are subject to the highest levels of mortality due to fishing. This is thought to be due to fishermen actively targeting larger individuals especially during the inshore migration period (Royer *et al.*, 2006). If adults are targeted more than juveniles later in the year this is beneficial to recruitment and ensures the size of the stock survives. However, if adults are targeted before spawning this could have a dire effect on the following year's recruitment and population (Royer *et al.*, 2006).

Global landings of cephalopods have increased from 0.5 million tonnes in 1958 to 4 million tonnes in 2008 (FAO 1964 & 2012). It is expected that landings will increase as fishing pressure subsequently increases following the decline of other marine stocks (Bloor *et al.*, 2013). Bloor & Jackson (2014) reported a change during the Marine Biological Association's scientific trawls from a dominance of *Sepia officinalis* to an increase in the less commercially important *Sepia elegans*. Further analysis is yet to be undertaken but this may suggest a shift in the dominant species.

There is evidence for low levels of genetic variation between populations from the Bay of Biscay, English Channel and southern North Sea (Wolfram *et al.*, 2006). However, they cannot be regarded as freely reproducing populations as there is still a lack of evidence of migration from the Bay of Biscay into the English Channel (Wolfram *et al.*, 2006). There is a significant correlation between geographical separation and increase in genetic distance between the waters of the Atlantic and Mediterranean (Perez-Losada *et al.*, 1999). The isolation is said to have occurred due to sea level changes during glacial maxima with a subsequent reconnection. This has led to subpopulations with restricted gene flow. The lack of genetic exchange is also a result of females fixing their eggs to the seafloor and a lack of a larval phase (Perez-Losada *et al.*, 2002).

Genetic, morphological and chemical differences have been seen between populations in Turkish coastal waters. The chemical structure of the cuttlebone has shown at least four geographical populations of *Sepia officinalis* amongst Turkish waters (Turan & Yaglioglu, 2010). These genetic differences may be due to the limited dispersal ability of *Sepia officinalis* alongside the lack of planktonic larval stage (Turan & Yaglioglu, 2010).

Sensitivity review

Resilience and recovery rates

Sepia officinalis has a short lifespan of between one to two years with mortality occurring shortly after spawning. This means that recruitment of the population relies heavily on the restocking of individuals to replace the mass mortality of adults after spawning (Hastie *et al.*, 2009, Challier *et al.*, 2006). This short, fast growing, lifespan means that each year's stock is almost entirely made up of one population, or two in the English Channel (Royer *et al.*, 2006).

Juveniles reach sexual maturity relatively early either in the following summer or the summer after depending on the temperature of water (Bloor *et al.*, 2013). Cultured *Sepia officinalis* are able to reproduce easily and are able to lay large eggs with a high chance of survival even under artificial conditions (Blanc *et al.*, 1999). There is usually only one breeding season for females before mortality occurs. Fecundity per individual is usually only 200-500 eggs and is size dependent (Boletzky, 1987). This is only thought to be 50% of their potential fecundity but the smaller number of eggs means the female can increase the energy yield of the internal yolk, allowing embryos to grow larger and stronger (Boletzky, 1987).

Sepia officinalis are also known as an 'intermittent terminal spawner'. This means they do not lay all of their eggs in a single place. Instead, they move up the coastline and spawn in particularly favourable conditions and environments. This increases the survival chance of the offspring (Rocha *et al.*, 2001). Eggs are also surrounded by ink from the female which acts as a protective barrier (Catarina *et al.*, 2017).

Maternal stress during spawning is likely to affect their offspring's phenotypes. Stress is associated with a reduction in offspring fitness and resistance to pressures such as disease (O'Brien *et al.*, 2017). Despite the lack of parental care post-hatching, the hatchlings are developed enough to begin actively feeding almost as soon as hatching is complete (Boletzky, 1983). The juveniles also show anti-predatory behaviour within the first few months including camouflage and burying (O'Brien *et al.*, 2017).

There is, therefore, a significant lack of overlap between generations. This leaves the species vulnerable to annual fluctuations in recruitments and stock size (Koueta *et al.*, 2000).

Complex recruitment

The annual variation in *Sepia officinalis* recruitment in the English Channel is estimated at 44-79 million individuals (Royer *et al.*, 2006). Successful recruitment requires sufficient breeding rates with a high survival of hatchlings (Boyle, 1990). There are also annual variations in recruitment and size at which maturity is reached (Gras *et al.*, 2016).

Females are polyandrous and therefore can accept sperm from multiple males, picking the sperm of choice to fertilize her offspring. This is beneficial as it means reproduction is not limited to a single, preferred male fertilizing all the females, and increases the chance of fertilization (Bloor *et al.*, 2013).

Environmental conditions

Sepia officinalis is not a vulnerable species to environmental conditions. On the contrary, the species tends to have a great ability to adapt to a range of different conditions (Sobrinho *et al.*, 2002). They do, however, require particular spawning habitats to ensure successful embryonic

development and hatching (Bloor *et al.*, 2013).

Sepia officinalis are efficient feeders and have tentacles which can reach prey within 15 milliseconds (Hanlon & Messenger, 1996). They are opportunistic feeders, eating a wide range of species allowing them to adapt to a variety of different prey (Jorge & Sobra, 2004). *Sepia officinalis* feeds on prey belonging to four different groups; polychaete, cephalopods, crustacean and bony fish. However, the variety of prey consumed decreases with an increase in size (Castro & Guerra, 1999). A group of starved cuttlefish were able to survive for up to 21 days post-hatching (Koueta & Boucaud-camou, 2001).

However, *Sepia officinalis* does not appear to have the ability to store food as energy in their tissues. If there is a restriction of food during early development it means sexual maturity will be reached later. This means they require a regular food supply in order to survive and more importantly reach sexual maturity and reproduce (Gras *et al.*, 2016). *Sepia officinalis* is also a very mobile species and therefore is able to move to another area which has more suitable conditions (Guerra, 2006).

Genetic differentiation

The restricted exchange in genetic information may lead to population specific variations in chemical structures and morphology (Carvalho and Hauser, 1994; Turan *et al.*, 2006; Turan & Yaglioglu, 2010). Such variations in morphology may affect the adaptability of *Sepia officinalis* to different environments. In areas of high water flow, individuals with bigger tentacular clubs and suckers have a better ability to cling onto rocks and avoid damage (Ozsoy *et al.*, 1996). The differences in morphology may limit different populations to certain areas restricting recruitment from neighbouring populations (Turan & Yaglioglu, 2010).

There appears to be a cross over in populations around the English Channel and the southern North Sea. However, there is a clear genetic difference between the Atlantic and Mediterranean populations (Wolfram *et al.*, 2006). In terms of recruitment, it appears that the lack of genetic similarity is due to a lack of movement of populations. This lack of external recruitment also occurs due to the lack of a larval pelagic stage (Pérez-Losada *et al.*, 2002).

Resilience. Recruitment to and recovery of populations is likely to be rapid depending on whether juveniles or adults are removed from the population and at what life stage this occurs. Therefore, recovery from any loss of the population (i.e. a reduction in the extent or abundance, i.e. resistance is 'Medium') may take up to 3-5 years for a replacement of population by a recovering generation. Hence, a resilience of '**Medium**' will be recorded. However, where the population is severely reduced in abundance or extent (i.e. resistance is 'None') a resilience of '**Very low**' will be recorded.

Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	Medium Q: High A: Medium C: Medium	Medium Q: Medium A: Medium C: Medium	Medium Q: Medium A: Medium C: Medium

Cephalopods have a poikilothermic metabolism that rises or falls directly with temperature (Forsythe, 1993; cited in Bloor *et al.*, 2013). For example, an increase of 6°C results in a doubling of individual feeding rate (Pascual, 1978). Cuttlefish in the English Channel have lower mitochondrial capabilities compared to subtropical Adriatic species but have larger hearts, which improve their energetic efficiencies. This allows them to extend their thermal tolerance (Oellermann *et al.*, 2012).

It has been estimated that the temperature limits of *Sepia officinalis* are 10 and 30°C (Guerra, 2006).

In the Ria Formosa, Portugal, water temperature reaches 27°C in the summer Lagoon system. The observed number of *Sepia officinalis* infers they can survive high water temperatures (Domingues *et al.*, 2002). Water temperature reached 30°C during the hottest day but no mortality was recorded. However, as temperatures rose in the Cíes Islands, Spain, the probability of finding eggs decreased. Instead, individuals in the Mediterranean prefer a spawning temperature of 12.5 – 14.75°C, similar to that of peak spawning in the English Channel (Guerra *et al.*, 2016b).

Embryonic development increases rapidly with an increase in temperature. At 17°C cultures, embryonic development took 56 days, resulting in a hatchling length of 8.4 mm mantle length (ML). In contrast, an increase in temperature to 20°C resulted in embryonic development taking just 40 days with hatchlings measuring a shorter 7.9 mm ML (Dickel *et al.*, 1997). Warmer waters are, therefore, associated with a shorter incubation time (Sykes *et al.*, 2006 b). However, a reduction in size could make the hatchlings more vulnerable to predation, reducing recruitment (Bouchaud, 1991).

Sensitivity assessment. *Sepia officinalis* appear to be able to withstand high temperatures. However, for an extended period of time, it could affect their behaviour, development and recruitment. Therefore, resistance is scored as '**Medium**'. Resilience is likely to be '**Medium**' and sensitivity is, therefore, '**Medium**'.

Temperature decrease (local)

Medium

Q: Medium A: Medium C: Medium

Medium

Q: Medium A: Medium C: Medium

Medium

Q: Medium A: Medium C: Medium

In the English Channel, water temperatures are known to get as low as 4°C in coastal areas (CEFAS, 2010, cited in Bloor *et al.*, 2013). A decrease in water temperature was directly correlated with the offshore migration of *Sepia officinalis* during winter months (Wang *et al.*, 2003). In the Adriatic Sea, where temperatures rarely fall beneath 12°C, no seasonal migration has been observed (Wolfram *et al.*, 2006). Individuals also reach sexual maturity later in colder waters (Boletzky, 1983), with a preferred spawning temperature of 9.5 – 20°C (Paulij *et al.*, 1990).

It has been estimated that the temperature limits of *Sepia officinalis* are 10 and 30°C. Below 10°C individuals do not appear to feed and remain inactive until ultimate mortality (Guerra, 2006). Individuals hatched in lower temperatures also have less inner yolk, presumably due to the increase in embryonic development time. This means once hatched the juveniles are under more pressure to gather food (Guerra, 2006). Embryos ceased development when cultured at 9°C. However, when the temperature was raised development continued, which suggested that eggs could almost go into a 'hibernation' period under lower temperatures. It is not known how long this period can last for before mortality (Bouchaud & Daguzan, 1990; Challier *et al.*, 2004). Oxygen demand for embryos is also increased at lower temperatures making embryos in colder water more susceptible to hypoxic conditions within the egg sac (Woods, 1999; cited in Lesser, 2013).

Sensitivity assessment: *Sepia officinalis* appear to be able to survive at low temperatures but suffer mortality after prolonged exposure to 10°C or lower. However, as temperatures decrease in coastal waters individuals may be expected to retreat to deeper waters, with the development of eggs and recruitment potentially affected. Therefore, resistance is scored as '**Medium**'. Resilience is likely to be '**Medium**' and sensitivity is, therefore, '**Medium**'.

Salinity increase (local) **High** **High** **Not sensitive**
 Q: Low A: NR C: NR Q: Medium A: Medium C: Medium Q: Low A: Low C: Low

Sepia officinalis inhabits oceanic waters that are of full salinity and is unlikely to experience an increase of salinity. In addition, this species is mobile and is, therefore, unlikely to remain in areas of salinity higher than 37 psu (e.g. from hypersaline effluents). Therefore, it is probably '**Not Sensitive**' at this benchmark level (i.e. resistance and resilience are '**High**')

Salinity decrease (local) **Medium** **Medium** **Medium**
 Q: Medium A: Medium C: Medium Q: Medium A: Medium C: Medium Q: Medium A: Medium C: Medium

Adults have been observed to tolerate brackish water, especially during inshore spawning periods. Adult individuals have been observed in the Ria de Vigo (NW Spain) where salinity in the inlet can range from 20-35 PSU. Despite this, eggs have been laid in this inlet (Guerra & Castro, 1998). Nevertheless, the preferred spawning salinity is reported to be 28 or greater (Paulij *et al.*, 1990).

Adult *Sepia officinalis* are able to survive in salinities of 18 PSU but only if acclimatised slowly (Guerra & Castro, 1988). However, adults are sufficiently mobile and are able to move to a new area if conditions are unfavourable. Juveniles are thought to have a higher plasticity to changes in salinity allowing them to live in more sheltered lagoons with higher freshwater influxes (Paulij *et al.*, 1990). However, normal embryonic development requires salinities above 24 ppt (Paulij *et al.*, 1990). Below 22.4 PSU malformed embryos were observed and the development rate of embryos was reduced even at 28.7 PSU. This is due to an increase in osmotic stress and a resultant reduction in available energy reserves (Paulij *et al.*, 1990). The highest percentage of healthy hatchlings was found at salinities of 29.8 PSU (Paulij *et al.*, 1990). Therefore, in culture, the optimum working salinity range is 27 – 35 PSU (Sykes *et al.*, 2006(b)).

Sensitivity assessment. It appears that adults and juvenile cuttlefish are able to survive in areas with a decrease from full salinity of ca. 10 PSU. However, embryos appear to be more sensitive to a decrease in salinity and adults can reduce their spawning or have a decreased growth rate. The short life span of this species, an annual reproductive cycle and its high fecundity means that recovery should take a year. Therefore, resistance to this pressure is '**Medium**'. Resilience is probably '**Medium**' and sensitivity is, therefore '**Medium**'.

Water flow (tidal current) changes (local) **High** **High** **Not sensitive**
 Q: Low A: NR C: NR Q: Medium A: Medium C: Medium Q: Low A: Low C: Low

Young hatchlings of only a month old responded to strong tidal currents by burrowing in the sand. Komak *et al.* (2005) reported a lack of migration and movement of juveniles under strong, turbulent, conditions. Therefore, it is important that juveniles have the ability to attach or bury deep enough in the substratum to withstand strong water movement (Boletzky, 1983). Adults were observed to align their bodies parallel to water flow when placed in a flow of 0.08 m/s even when this opposed the pattern of the background (Shohet *et al.*, 2006).

Sensitivity assessment. *Sepia officinalis* does not appear to be negatively affected by a change in tidal current, therefore, this species is probably '**Not Sensitive**' with a '**High**' resistance and a '**High**' resilience.

Emergence regime changes **High** **High** **Not sensitive**
 Q: High A: High C: High Q: High A: High C: High Q: High A: High C: High

Sepia officinalis are sublittoral and so will not be affected by an increase in emergence at the benchmark level. The species is fast moving and will avoid emergence. *Sepia officinalis* embryos encased in eggs can be transported for culture for up to 8.5 h in damp or dry conditions or in seawater. Observations of a reduction in oxygen consumption are thought to protect the developing embryos from the damp and dry conditions. The survival rate of transported eggs was 83 – 86% for both eggs kept in water or in dry conditions (Jones *et al.*, 2009).

Sensitivity assessment. Therefore, resistance is probably '**High**', resilience is '**High**' (by default) and this species is assessed as '**Not Sensitive**' at the benchmark level.

Wave exposure changes (local) **High** **High** **Not sensitive**
 Q: Medium A: Medium C: Medium Q: Medium A: Medium C: Medium Q: Medium A: Medium C: Medium

In rough weather, cuttlebones are often found washed up on beaches. This may mean that some of the population are destroyed when wave exposure increases or it could cause the already, naturally, deceased to wash up. Despite these observations, the species is sufficiently mobile to be able to move to deeper water if conditions are unfavourable. Therefore, resistance is probably '**High**', resilience '**High**' (by default) and this species is assessed as '**Not Sensitive**' at the benchmark level.

Chemical Pressures

	Resistance	Resilience	Sensitivity
Transition elements & organo-metal contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
'Not Assessed'			
Hydrocarbon & PAH contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
'Not Assessed'			
Synthetic compound contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
'Not Assessed'			
Radionuclide contamination	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR
No evidence			
Introduction of other substances	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
'Not Assessed'			

De-oxygenation**Medium**

Q: Medium A: Medium C: Medium

Medium

Q: Medium A: Medium C: Medium

Medium

Q: Medium A: Medium C: Medium

Sepia officinalis survived 60 mins in tanks at 50% of normal dissolved oxygen, 16.28 mg/l (Capaz *et al.*, 2017). However, *Sepia officinalis* reduced their oxygen consumption to 37% and increased their ventilation rate to 85%. Metabolic rate subsequently decreased and a minor increase in anaerobic respiration was shown by an accumulation of octopine (lactic acid) (Capaz *et al.*, 2017).

Surprisingly, there was no recorded stress response of the animal (no increase in heat-shock protein 70). Capaz *et al.* (2017) suggested a lack of stress associated with a decrease in dissolved oxygen. Oxygen extraction from ambient water at 17°C is thought to be 70% (Melzner *et al.*, 2006). Cephalopods also appear to have a more highly closed pressurised vascular system compared to other molluscs allowing them to distribute the O₂ taken up by the gills (Häferker, 2012).

Sepia officinalis will be vulnerable to areas of hypoxia when migrating inshore to sheltered bays and estuaries in order to spawn (Guerra, 2006). Boletzky (1981) suggested that the oxygen saturation of the surrounding water must be close to full saturation for efficient development and successful sexual maturity. *Sepia officinalis* embryos are encased in a protective egg-case which protects it from infection, certain predation and acts as a barrier for gas diffusion (Cronin & Seymour, 2000, Catarina *et al.*, 2017). During the end of embryonic development, oxygen consumption significantly increases, relying heavily on a good supply of dissolved oxygen from the surrounding waters at levels as close to saturation as possible (Cronin & Seymour, 2000). *Sepia officinalis* embryos encased in eggs can be transported for culture for up to 8.5 hr in damp or dry conditions or in seawater. A reduction in oxygen consumption is thought to protect the developing embryos from the damp and dry conditions. The survival rate of transported eggs was 83 – 86% for both eggs kept in water or in dry conditions (Jones *et al.*, 2009). It must be reminded that this is a mobile species and, therefore, after hatching the likelihood of remaining in an area of low oxygen is unlikely.

Sensitivity assessment. *Sepia officinalis* appears to be adapted to survive in a dissolved oxygen concentration of 16.28 mg/l by reducing their oxygen consumption or moving away from the area. This, however, is higher than the benchmark of 2 mg/l for this pressure. De-oxygenation is thought to affect the development of embryos. Therefore resistance is assessed as '**Medium**' due to the potential effect on recruitment. Resilience is probably '**Medium**' and sensitivity is, therefore '**Medium**'.

Nutrient enrichment**High**

Q: Low A: NR C: NR

High

Q: Medium A: Medium C: Medium

Not sensitive

Q: Low A: Low C: Low

Refers to the increased levels of nitrogen, phosphorus and silicon in the marine environment. Nutrient enrichment from pollution and other sources can lead to an increase in algal blooms. In turn, this can lead to periods of deoxygenation (see deoxygenation pressure). No evidence on the effect of nutrient enrichment specific to this species was found. However, the species is considered to be '**Not sensitive**' at the pressure benchmark that assumes compliance with WFD criteria for good status.

Organic enrichment**High**

Q: Low A: NR C: NR

High

Q: Medium A: Medium C: Medium

Not sensitive

Q: Low A: Low C: Low

Organic enrichment encourages the productivity of suspension and deposit feeding detritivores and allows species to colonize the affected area to take advantage of the enhanced food. Suspended

organic material in the water column will eventually settle on the seabed. However, this has the potential to deoxygenate the benthic environment due to the decomposition of the material causing hypoxia (Riera *et al.*, 2013). *Sepia officinalis* is mostly a mobile demersal species and will probably avoid areas if hypoxia. Therefore the pressure for this species at this benchmark is likely to be '**Not Sensitive**' (see de-oxygenation).

A Physical Pressures

	Resistance	Resilience	Sensitivity
Physical loss (to land or freshwater habitat)	Medium Q: Low A: NR C: NR	Medium Q: Medium A: Medium C: Medium	Medium Q: Low A: Low C: Low

Adult *Sepia officinalis* are able to migrate from offshore habitats to inshore, but can also choose where they would like to lay their eggs. This means that if an environment is not suitable, the individual will continue moving in order to find a more suitable location to live and/or spawn (Bloor *et al.*, 2013).

Eggs, hatchlings and juveniles are more vulnerable to the permanent loss of a habitat due to their preference for a particular environment (Camou, 2001). If a structure was to suddenly be placed or an area of land claimed then this would result in the immediate mortality of any small individuals/eggs in that area. Without shallow, sandy, areas recruitment potential may be reduced due to limitation for space and resources (see habitat removal).

Sensitivity assessment. Adults are unlikely to be directly affected by the physical loss of an area as they have highly mobile abilities. Juveniles, hatchlings and eggs are more vulnerable to immediate mortality and a lack of available habitat to survive. Therefore, the resistance is assessed as '**Medium**' but with 'low' confidence. Resilience is probably '**Medium**' and sensitivity is, therefore, '**Medium**'.

	Resistance	Resilience	Sensitivity
Physical change (to another seabed type)	Medium Q: Medium A: Medium C: Medium	Medium Q: Medium A: Medium C: Medium	Medium Q: Medium A: Medium C: Medium

Hatchlings bury themselves in response to threats (e.g. predators) due to their lack of ability to camouflage or flee (O'Brien *et al.*, 2017). Therefore, newly hatched embryos and developing juveniles require sandy substrata to avoid predation. Duration of digging also takes far longer in gravel compared to fine sand and some cuttlefish even refuse to bury into gravel making them vulnerable to predation (Mather, 1986). Juveniles and eggs are usually placed in sheltered areas such as seagrass beds. This reduces their vulnerability to predation and the impact of tides and water surges (Jackson *et al.*, 2001). Without such shelters mortality is likely to occur, reducing recruitment. A lack of an appropriate environment for offspring may result in the female choosing not to lay any eggs at all reducing potential recruitment for the following population (Bloor *et al.*, 2013). However, adults are highly mobile and, therefore, unlikely to be affected by a change in substratum since it can relocate to more favourable conditions.

Sensitivity assessment. Resistance is probably '**Medium**', however, confidence is 'Low' due to lack of evidence of mortality. Due to the lack of overlap in generations, survival of hatchlings is vital for replenishment and recruitment, therefore, resilience is considered '**Medium**' and sensitivity is assessed as '**Medium**'.

Physical change (to another sediment type)**Medium**Q: **Low** A: **NR** C: **NR****Medium**Q: **Medium** A: **Medium** C: **Medium****Medium**Q: **Low** A: **Low** C: **Low**

Adult *Sepia officinalis* will not be affected by a change in sediment class due to the species being highly mobile. However, juveniles rely heavily on sandy bottoms in order to shelter and hide from predation (see juveniles). A change in sediment class has not, however, shown to result directly in an increase in mortality rates.

Sensitivity assessment. Hatchlings and juveniles are probably the most vulnerable to this pressure, as a change to muddy, coarse or hard substratum may increase their vulnerability to predation, therefore, resistance is assessed as '**Medium**' but with 'Low' confidence due to a lack of evidence. Resilience is probably '**Medium**' and sensitivity is, therefore, '**Medium**'.

Habitat structure changes - removal of substratum (extraction)**Low**Q: **Low** A: **NR** C: **NR****Medium**Q: **Medium** A: **Medium** C: **Medium****Medium**Q: **Low** A: **Low** C: **Low**

The act of physically removing the substratum e.g. by dredging may affect the cuttlefish (see physical disturbance). The ability of juveniles to attach themselves onto hard substratum is very important in ensuring they can withstand strong water movements (Boletzky, 1983). Juveniles and hatchlings also need to burrow into sandy substratum in order to avoid predation (Boletzky, 1983). There is also the risk that hatchlings and eggs buried or attached to the substratum will be removed along with the substratum resulting in mortality.

Sensitivity assessment. The loss of habitat is unlikely to affect mobile adults but may damage or remove eggs, hatchlings and/or juveniles, reducing recruitment and further spawning due to a lack of suitable substratum. Therefore, resistance is likely to be '**Low**' but with 'low' confidence due to a lack of evidence. Resilience is probably '**Medium**' and sensitivity is, therefore, '**Medium**'.

Abrasion/disturbance of the surface of the substratum or seabed**Low**Q: **Low** A: **NR** C: **NR****Medium**Q: **Medium** A: **Medium** C: **Medium****Medium**Q: **Low** A: **Low** C: **Low**

Cuttlefish have a soft, unarmoured body making them vulnerable to damage and injury (Hanlon & Messenger, 1991; Cooke & Tonkins, 2015). The cuttlebone is able to repair itself and maintains buoyancy so that cuttlefish can withstand a certain amount of internal bone injury (Boletzky & Overath, 1991).

Individuals observed after mating and after entanglement in nets typically have soft tissue damage that suggests susceptibility to abrasive damage (Guerra *et al.*, 2016b). In a southern otter trawl, 77% of the landed *Sepia officinalis* were discarded suggesting high levels of damage occurring from these trawls (Guerra *et al.*, 2016b). CEFAS has recorded discards of cuttlefish in the English Channel from 6% to 23% of total catch since 2002 (ICES, 2012). Enever *et al.* (2007) showed that *Sepia officinalis* was the second most discarded species under the top ten most discarded English Channel species by beam trawlers.

Sepia officinalis from a large beam trawler operating in the offshore waters of south-west UK were examined during a single fishing trip for signs of damage and survival (Revill, 2011). Analysis showed that 16% of these small cuttlefish (< 15 cm) died later after their injuries from capture, 68% died whilst in the trawl or on the deck, and only 16% survived capture and deck sorting and were

expected to survive discarding (Revell, 2011). Individuals with mantle lesions and trauma are also susceptible to developing bacterial sepsis (Sherrill *et al.*, 2000). However, the short life-span of this species, its annual reproduction and its high fecundity means that population recovery from such effects should occur after a year.

Abrasion, due to trawling and dredging, may also remove biogenic structures such as seaweed and seagrass which are locations of attached eggs. If eggs have already been laid they are likely to be destroyed and the area is left as an unfavourable spawning ground (Bloor & Jackson, 2014).

Sensitivity assessment. Adults are able to move out of the way of a lot of danger but are at risk of being caught and/or damaged by fishing equipment. However, juveniles and eggs are more vulnerable due to their reduced ability to move out of the way. Therefore, resistance is assessed as 'Low' but with 'low' confidence. Resilience is probably 'Medium' and sensitivity is assessed as 'Medium'.

Penetration or disturbance of the substratum subsurface

Low

Q: Low A: NR C: NR

Medium

Q: Medium A: Medium C: Medium

Medium

Q: Low A: Low C: Low

Sepia officinalis is a mobile species and therefore is not likely to be affected by penetration by fishing gear, dredges or other activities. However, the primary defensive behaviour of juveniles or smaller, weaker, individuals is to bury into the sandy sea-floor. Penetration could therefore directly injure or damage the buried individual, affecting the recruitment rates for the population. Therefore, based on the evidence above (abrasion), resistance is assessed as 'Low' but with 'low' confidence. Resilience is probably 'Medium' and sensitivity is assessed as 'Medium'.

Changes in suspended solids (water clarity)

High

Q: Low A: NR C: NR

High

Q: Medium A: Medium C: Medium

Not sensitive

Q: Low A: Low C: Low

Sepia officinalis may benefit from reduced water clarity by acting as an external camouflage so that the species can preserve more energy. This may help reduce the chances of predation especially on the eggs of *Sepia officinalis* (Catarina *et al.*, 2017). But, suspended solids may inhibit the species from effectively feeding by removing visual cues (Mäthger *et al.*, 2006) as well as interfere with mating rituals. However, *Sepia officinalis* is a highly intelligent animal and is able to use other cues, such as chemical or audial, in order to track down prey and other individuals (Samson *et al.*, 2014). Juveniles are able to catch shrimps with ease in complete darkness (Blanc *et al.*, 1998). Furthermore, Jozet-Alves *et al.* (2013) suggested that *Sepia officinalis* may have an episodic-memory allowing the cuttlefish to remember key prey hotspots and feeding locations.

Sensitivity assessment. Resistance is likely to be 'High' but with 'low' confidence. Resilience is probably 'High' and sensitivity is, therefore, assessed as 'Not sensitive'.

Smothering and siltation rate changes (light)

High

Q: Medium A: Medium C: Medium

High

Q: Medium A: Medium C: Medium

Not sensitive

Q: Medium A: Medium C: Medium

The species is highly mobile and therefore unlikely to be affected by smothering since it can relocate to more favourable conditions. Juveniles are also able to move and dig into and out of small and large grain sand (Boletzky, 1983). Eggs are usually laid on floating or suspended structures in the water column and therefore are unlikely to be affected by light sediment deposition (Bloor *et al.*, 2013).

Sensitivity assessment. Resistance is, therefore, likely to be 'High'. Resilience is 'High' by default and sensitivity is therefore assessed as 'Not sensitive'.

Smothering and siltation rate changes (heavy) **High** **High** **Not sensitive**
 Q: Medium A: Medium C: Medium Q: Medium A: Medium C: Medium Q: Medium A: Medium C: Medium

The species is highly mobile and therefore unlikely to be affected by smothering since it can relocate to more favourable conditions. Juveniles are also able to move and dig into and out of deposited sediment (Boletzky, 1983). The duration of the digging and the juvenile's ability to dig depends on the sediment (Mather, 1986). If there is a heavy deposition of coarse sand then juveniles should be able to dig straight out. As this benchmark is for the deposition of fine material and not hard gravel like substrata, there should be relatively low, if any, impact on the juveniles (Mather, 1986). Eggs are usually laid on floating or suspended structures in the water column and therefore are unlikely to be affected by heavy sediment (Bloor *et al.*, 2013).

Sensitivity assessment. Resistance is therefore likely to be 'High'. Resilience is probably 'High' and sensitivity is, therefore 'Not sensitive'.

Litter **Not Assessed (NA)** **Not assessed (NA)** **Not assessed (NA)**
 Q: NR A: NR C: NR Q: NR A: NR C: NR Q: NR A: NR C: NR

'Not assessed'. However, it is noted that man-made objects that have been left or dumped into the sea, such as ropes, are a popular spot for *Sepia officinalis* females to attach their eggs.

Electromagnetic changes **No evidence (NEv)** **Not relevant (NR)** **Not relevant (NR)**
 Q: NR A: NR C: NR Q: NR A: NR C: NR Q: NR A: NR C: NR

'No evidence'

Underwater noise changes **Medium** **Medium** **Medium**
 Q: Low A: NR C: NR Q: Medium A: Medium C: Medium Q: Low A: Low C: Low

The statocyst is considered the primary sound detection organ in cephalopods. Alongside peripheral hairs and epidermal hairs, *Sepia officinalis* is able to detect local water movement by detecting vibrations (Hanlon & Messenger, 1996; Samson *et al.*, 2014). The statocyst is also responsive for equilibrium and movement in the water column (Solé *et al.*, 2017).

In aquarium facilities in Portaferry, Northern Ireland, 30 individual *Sepia officinalis* were subject to 210 seconds of playback of engine noise recorded from a car ferry (165 Db). The noise appeared to affect the colour changing behaviour and movement of the cuttlefish. Individuals changed colour more frequently and increased locomotion compared to a control group with a playback of ambient reef noises. These behaviours suggested an increase in stress level (Kunc *et al.*, 2014). As cephalopods use complex movements and behaviour during courtship, mating and camouflage, noise pollution may increase predation risk and decrease the chances of reproduction (Kunc *et al.*, 2014).

Noise was also reported to increase occurrences of jetting and inking (Hanlon & Messenger, 1996). The greatest intensity response e.g. inking, was found at the highest sound levels (100-300 Hz) (Samson *et al.*, 2014) and above 140 Db. *Sepia officinalis* was able to habituate (get used to) the noise when identical sounds were played close together (Samson *et al.*, 2014). This observation

suggested that *Sepia officinalis* would not show a long-term response to sound.

Individuals exposed to levels of sound from 139-142 dB centred at 315-400 Hz revealed injuries to the statocyst. Immediately after exposure to the sound, spherical holes were found on the base of the hair cells and in the plasma membrane of the statocyst. After 48 h of sound exposure damage occurred on the internal epithelium and some hair cells were either partially or totally ejected from the sensory epithelium. This could result in permanent physical damage but due to the dissections needed for this study the long-term effects are still unknown (Solé *et al.*, 2017). If the species is disturbed by noise it should swim away when it senses any vibrations. The viability of the species may be reduced if feeding or breeding periods are disrupted.

Sensitivity assessment. *Sepia officinalis* are able to undergo habituation to the sound but may change their behaviour, including mating behaviour. Internal damage has been caused by specific noise levels, meaning, the resistance to this pressure is probably 'Medium' albeit with 'low' confidence. Hence, resilience is probably 'Medium', and sensitivity has been assessed as 'Medium'.

Introduction of light or shading

High

Q: Low A: NR C: NR

High

Q: Medium A: Medium C: Medium

Not sensitive

Q: Low A: Low C: Low

Sepia officinalis appears to be sensitive to light. Under a bright light in Plymouth Marine Laboratory, the species buried themselves under gravel at the bottom of the tank. Under an artificial light, that mirrored natural diffused daylight, adults showed increases in density (Denton & Gilpin-Brown, 1961). However, burying did not occur all the time during the periods of light exposure. If large cuttlefish were hungry, or if two males were in the same tank, they entered mid water and remained there even under high light intensity.

Sexual migration is not always determined by temperature. Individuals have been seen to leave warmer waters and arrive in April when waters are still only 10°C. It is thought that photoperiod plays a role in determining the time at which sexually mature individual's migrate back inshore (Boucaud-Camou & Boismery, 1991). The photoperiod is the length of daily illumination received by the individual (Koueta *et al.*, 2005). In the English Channel, therefore, inshore migration usually occurs around the spring equinox when the daily photoperiod increases (Koueta and Boucaud-Camou, 2003).

Hatching is also determined by the transition from light to dark (Koueta and Boucaud-Camou, 2003). Therefore, the absence of light is very important in synchronised hatching (Paulik *et al.*, 1991) and reduced predation. Under a low photoperiod in a lab (8 h of light and 16 h of dark) growth rates were low for juveniles. Long photoperiods (24 h of light) in aquaculture resulted in a longer lifespan and larger individuals. However, gonad development appeared to be inhibited, allowing the animal to live longer but prohibited reproduction (Forsythe *et al.*, 1994).

Cuttlefish adjust their camouflage depending on light intensity. In extremely low light (<0.001 lux) cuttlefish do not camouflage but instead retract their dermal chromatophores and choose a pale appearance, suggesting a low energy response (Buresch *et al.*, 2015). Under high light intensity camouflage is increased with more energy consumption. A danger of the increase in an extended period of illumination is that more energy will have to be prioritised for camouflage and not other processes such as growth or reproduction (Buresch *et al.*, 2015).

Sensitivity assessment. Despite showing a behavioural response to light there is no evidence of death due to the effect of an introduction of light from an artificial source. Therefore, a resistance

score of 'High' is recorded with 'low' confidence. Recoverability is probably 'High' and this species is therefore assessed as 'Not Sensitive' to the induction of light or shading

Barrier to species movement

None

Q: Low A: NR C: NR

Very Low

Q: High A: High C: High

High

Q: Low A: Low C: Low

There is evidence of gene flow between the English Channel and southern North Sea populations probably due to the mobility of this species. However, there is also clear genetic differences between the Atlantic and Mediterranean populations (Wolfram *et al.*, 2006).

Sensitivity assessment. *Sepia officinalis* migrates to deep water to breed and returns to coastal waters to spawn. A barrier to movement (e.g. barrage) is likely to prevent this migration and, since the species has a short lifespan, result in loss of the local population affected by the barrier. If the barrier is temporary then recovery may be rapid (a few years). However, a permanent barrier may exclude *Sepia officinalis* from the affected area. Therefore, in the worst-case scenario of a permanent barrier, resistance is probably **None**, and a resilience is '**Very low**' (as the barrier is permanent) and sensitivity is assessed as '**High**'. However, confidence in the assessment is 'low'.

Death or injury by collision

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Collision with the individual due to grounding by vessels is addressed under (abrasion). Therefore, this pressure is '**Not relevant**'.

Visual disturbance

High

Q: Medium A: Medium C: Medium

High

Q: Medium A: Medium C: Medium

Not sensitive

Q: Medium A: Medium C: Medium

Sepia officinalis have the ability to perceive and differentiate different objects from their background as long as they differ in contrast from the background by at least 15% (Mäthger *et al.*, 2006). They are thought to have just one visual pigment that has a maximum adsorption of green light (492 nm) (Mäthger *et al.*, 2006). *Sepia officinalis* are thought to have reasonable 'night-vision', due to their nocturnal hunting and feeding behaviour (Castro & Guerra, 1989).

The species also appears to be colour-blind due to their inability to camouflage against and distinguish certain visual cues (Mäthger *et al.*, 2006). When placed on a checkerboard of alternating blue and yellow shades of the same intensity, cuttlefish did not show a disruptive colouration suggesting it was unable to differentiate between the two colours of the same light intensity (Mäthger *et al.*, 2006).

It has been proposed (John Rundle, personal communication, cited in Tonkins *et al.*, 2015) that dark figures leaning over tanks may be interpreted as predators by captive cuttlefish. This may lead to a defence response such as digging, swimming, and inking.

Sensitivity assessment. The species has well-developed eyes so can detect movement sufficiently well to be susceptible to visual disturbance. However, the species will swim away or hide when any presence threatens, therefore, recovery is immediate. Visual cues may cause a behavioural response but due to the mobility of the species, the pressure is unlikely to cause mortality or interfere with reproduction. Hence, resistance is '**High**', resilience is '**High**', and the species is likely to be '**Not sensitive**'.

Biological Pressures

	Resistance	Resilience	Sensitivity
Genetic modification & translocation of indigenous species	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

There is evidence of gene flow between the English Channel and southern North Sea populations probably due to the mobility of this species. However, there is also clear genetic differences between the Atlantic and Mediterranean populations (Wolfram *et al.*, 2006). Therefore, translocation of specimens between Mediterranean and Atlantic population may affect the genotypes of the resident populations. However, there is no evidence that this has or is likely to occur and no evidence to suggest that it would be detrimental for the receiving population. Therefore, the pressure is probably '**Not relevant**'.

Introduction or spread of invasive non-indigenous species	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR
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The invasive blue crab *Callinectes sapidus* is originally from the coasts of the western Atlantic but has now reached European waters. It inhabits the same habitat niche of sandy bottoms at 35 m in depth as *Sepia officinalis*. In culture, it has also shown to actively feed on *Sepia officinalis* eggs. This crab has the potential to be a risk to *Sepia officinalis* but there is currently no evidence of actual introduction, therefore '**No evidence**' is recorded (Catarina *et al.*, 2017).

Introduction of microbial pathogens	Medium Q: High A: Medium C: Medium	Medium Q: Medium A: Medium C: Medium	Medium Q: Medium A: Medium C: Medium
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Some bacteria are not pathogenic but are in fact symbiotic and occur in the accessory rudimental gland in cuttlefish (Grigioni & Boucher-rodoni, 2002). It is thought that these bacteria are responsible for the colour change in the gland from white to bright red/orange which signifies the individual is sexually mature (Grigioni & Boucher-Rodoni, 2002). *Sepia officinalis* also has naturally occurring Gammaproteobacteria, e.g. *Vibrionaceae*, in the gills and oesophagus. These bacteria appear to be resilient to the common animal antibiotic enrofloxacin (Lutz *et al.*, 2018).

A common infection spot in *Sepia officinalis* is in the digestive tract and stomach epithelium (Hanlon & Forsythe, 1990). A virus similar in structure to a retrovirus in vertebrates was found in the stomachs of wild cuttlefish (Hanlon & Forsythe, 1990). Microbes were recorded on the outside of *Sepia officinalis* egg cases that reduced the oxygen available to diffuse into the egg (Cronin & Seymour, 2000).

The coccidian *Aggregata eberthi* appears to use the digestive tract of the cuttlefish as part of their sexual reproduction (Gestal *et al.*, 2002). This has been known to lead to an increase in gut infections, which reduces the function of the digestive system and limits the absorption of nutrients (Gestal *et al.*, 2002). However, there is little evidence of direct mortality as a result of microbial infection (Hochberg, 1990).

Fungal infections can appear on *Sepia officinalis* but these are usually the result of trauma to the skin or a weakening of the immune system (Harms *et al.*, 2006). Cells known as ovoid cells in the heart tissue are known to target bacterial toxins in the blood. This shows a strong immune

response to microbial infection and suggests a tolerance to them (Beuerlin & Schipp, 1998).

Despite their resistance, inflammation and secondary bacterial infections occur generally in cuttlefish that have sustained trauma or mantle lesions. Septicaemia (*Vibrio spp.*) caused by mantle erosion from trauma and/or collision resulted in the death of 4/7 cultured cuttlefish under standard culturing conditions (Sherrill *et al.*, 2000).

Sensitivity assessment. *Sepia officinalis* appear to be relatively tolerant to microbial infections but once damaged due to trauma appear less resistant, resulting in a score of 'Medium'. Recovery is probably 'Medium' and sensitivity is, therefore 'Medium'.

Removal of target species

Low

Q: Medium A: Medium C: Medium

Medium

Q: Medium A: Medium C: Medium

Medium

Q: Medium A: Medium C: Medium

In many areas, *Sepia officinalis* is fished at the maximum sustainable rate but in others, there has been a recent decline in captures in heavily fished areas. It is the most abundant cephalopod species fished in the North East Atlantic with annual landings ranging from 40,000-50,000 (ICES, 2009). The UK cuttlefish landings for UK vessels in 2015 was ca. 6000 tonnes (MMO, 2016; cited in ICES, 2017(b)). The primary mode of fishing is trawling but cuttlefish are also caught by artisanal fisheries using pots and traps (ICES, 2003). The peak inshore fishing season, unfortunately, coincides with the peak spawning period meaning adults have a limited time to reproduce and replenish the subsequent population before they are fished (ICES, 2003).

In inshore French waters, *Sepia officinalis* is harvested by traps that selectively remove males prior to reproduction, trawls that capture a high percentage of females and juveniles, and nets that capture an even ratio of adult males and females (du Sel *et al.*, 1997). Females have been shown to mate with multiple males meaning a reduction in males may not affect the fecundity of the population drastically.

Sepia officinalis eggs are removed unintentionally as the females attach them to cuttletraps from March to September. The fishermen, fishing for adult cuttlefish, do not tend to place the traps straight back into the ocean and instead leave the traps and eggs on the pontoon to be desiccated (Blanc & Daguzan, 1998). Due to the lack of generation overlap, the mortality of eggs is detrimental to the recruitment of the population.

There is an issue of high discarding rates within the cephalopod fisheries. In 2008, an estimated 306 tonnes of small cuttlefish were discarded in the south-west of England (CEFAS; cited in Revill, 2011). From interviews with fishermen, a major reason for discarding juveniles is the hope that they will grow bigger and to a more valuable size for the following years capture (Revill, 2011). *Sepia officinalis* from a large beam trawler operating in the offshore waters of south-west UK were examined during a single fishing trip for signs of damage and survival (Revill, 2011). Analysis showed that 16% of these small cuttlefish (<15 cm) died later after their injuries from capture, 68% died whilst in the trawl or on the deck, and only 16% survived capture and deck sorting and were expected to survive discarding (Revill, 2011).

There is currently no routine monitoring or assessment scheme in place for the English Channel *Sepia officinalis* stock (Gras *et al.*, 2014). During the sea trials, large cuttlefish were able to survive the trauma of trawling and deck sorting more than the delicate smaller cuttlefish. The damage to the smaller cuttlefish was damage to the skin and even internal cuttlebone suggesting smaller cuttlefish are more fragile and weaker than adults (Revill, 2011). As there is no current minimum

landing size of cuttlefish in the UK. Therefore small cuttlefish are more vulnerable to catch and discarding than adults (British Sea Fishing, 2018).

Landings are also increasing globally. For example, in the English Channel, total annual landings have increased from 430t in 1992 to 17,400t in 2014 (Gras *et al.*, 2016). Dunn (1999) suggested that as the market value is increased, cephalopods could becoming more popular for fishermen, which may begin to hinder *Sepia officinalis* stocks in the future.

Sensitivity assessment. *Sepia officinalis* have 'Low' resistance to removal. Resilience is likely to be 'Medium' as there is no current recorded global decline in stocks. However, stocks of *Sepia officinalis* are currently able to just about continue replenishing the current population but if fishing pressures increase the likelihood of replenishment will be reduced (ICES, 2017(b)). Sensitivity is, therefore, 'Medium'.

Removal of non-target species

Medium

Q: Low A: NR C: NR

Medium

Q: Low A: NR C: NR

Medium

Q: Low A: Low C: Low

Extraction of another species will not have a strong effect on this species as their prey is very varied and they have no dependence on one particular species. *Sepia officinalis* have a varied diet from amphipods to gobies and sand eels. In extreme cases, they may even become cannibalistic, preying on smaller individuals (Castro & Guerra, 1990). Prey size is also selective, with adult *Sepia officinalis* choosing fish 25-80% and crabs 20-40% the size of their mantle length (Blanc *et al.*, 1999). Predators of *Sepia officinalis* include; sharks, lobsters and other cephalopods (Catarina *et al.*, 2007). The extraction of non-target species is not thought to affect *Sepia officinalis* from a biological point of view. Instead, the biggest risk to the species due to this removal is; removal of eggs by accident (see abrasion) and by-catch.

In the Mersin province, Turkey, 10g of *Sepia officinalis* were caught as by-catch using one trawl from September 2004 to April 2005. The target fish were; mullet, goatfish and shrimp (Atar & Malal, 2010). In Algarve (southern Portugal), *Sepia officinalis* are occasionally caught in tuna traps (Neves dos Santos *et al.*, 2002). Many eggs are laid on cuttletraps during spawning periods. When removed from water fishermen are not interested in collecting the eggs. Instead, they are usually left on the pontoon until further use resulting in either mortality or significant damage (Blanc & Daguzan, 1998).

Sensitivity assessment. Resistance is probably 'Medium' but with 'Low' confidence due to a lack of available by-catch figures. Resilience is probably 'Medium' and sensitivity is 'Medium'

Importance review

Policy/legislation

IUCN Red List Least Concern (LC)

★ Status

National (GB) importance	-	Global red list (IUCN) category	Least Concern (LC)
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Non-native

Native	Native		
Origin	-	Date Arrived	N/A

Importance information

Cephalopods are known for their intelligence (Hastie *et al.*, 2009). *Sepia officinalis* has the ability to camouflage and undertake learned behaviour. *Sepia officinalis* can also alter their buoyancy by controlling how much liquid is placed into or out of the cuttlebone (Denton & Gilpin-Brown, 1961). Dunn (1999) and Gutowska *et al.*, (2008) reported that an increase in pCO₂, and therefore a decrease in pH, appeared to have no effect on the ability to calcify the cuttlebone. Therefore *Sepia officinalis* may be well adapted to deal with the issue of ocean acidification to a moderate level.

In terms of ecological value, *Sepia officinalis* appears to play a dominant role in the marine food chain (Boletzky & Hanlon, 1983). *Sepia officinalis* have also been shown to have antimicrobial agents in their body tissue and cuttlebone. These agents were able to increase the survival rates of CLP-septic (cecal ligation and puncture) rates by 66.7 – 83.33%. This may be due to the chelating activity of the body tissues which may prevent further growth of pathogens (Soilman *et al.*, 2016).

Ethics

Cephalopods are “recognized as advanced organisms capable of pain and suffering and were recently added to the list of protected animal groups covered by European welfare legislation” (Directive 2010/63/EU). Since 1st January 2013, all cephalopods have been protected under UK/EU law (A (SP) A1986, European Directive 2010/63/EU).

Fishing

Sepia officinalis is the most abundant cephalopod resource in the North East Atlantic. Cephalopod annual landings have ranged from 40,000 – 50,000 tonnes from 1999-2009 (ICES, 2009). Of these landings, cuttlefish accounted for 16,000 to 24,000 tonnes annually (Hastie *et al.*, 2009). *Sepia officinalis* accounted for a large proportion of these landings. It is also one of the three most valuable resources for the English Channel Fisheries (Gras *et al.*, 2014). The UK cuttlefish landings for UK vessels in 2015 was ca. 6000 tonnes (MMO, 2016; cited in ICES, 2017(b)).

In the English Channel, landings of *Sepia officinalis* have increased from 430 t in 1992 to 17,400 t in 2014 (Gras *et al.*, 2016). This increase was driven by an increase in the market value of cuttlefish during the 1980 s from £0.40 per kg to £1.10 per kg (Dunn, 1999).

In the Archipelago of Madeira, the total landings appear to fluctuate annually. For example, the total landings of *Sepia officinalis* in Madeira ranged from 1978 t in 2013 to 1052 t in 2015 (Guerra

et al., 2016b). Due to the commercial value and lack of landing restrictions, individuals are only discarded if damaged. In a southern otter trawl, 77% of the landed *Sepia officinalis* were discarded, suggesting high levels of damage occurring from these trawls (Guerra *et al.*, 2016b). However, the species is also recorded as one of the species with high levels of unreported catches (Batista *et al.*, 2015).

Protection

The English Channel is dominated by offshore trawlers accounting for 90% of the UK landings of cephalopods, whereas inshore traps contribute to only 5% of UK landings (ICES, 2003). Inshore landings are higher between March and June, corresponding to the peak in the spawning season. However, this means that *Sepia officinalis* are fished during their most vulnerable spawning period, vital for recruitment (ICES, 2003). There is currently no routine monitoring or assessment scheme in place for the English Channel *Sepia officinalis* stock (Gras *et al.*, 2014, ICES, 2017(b)). Cephalopod fisheries are continuing to expand in Europe, declining marine stocks (Turan & Yaglioglu, 2010).

Cephalopods, including *Sepia officinalis*, have been reported to benefit from local bans on trawling, increasing mesh size and banning the fishing in certain shore areas from operating within three nautical miles of the shore (Gras *et al.*, 2014). Protection has also occurred through the trial of more selective fishing gears including net modifications (e.g. larger mesh size). The results showed the net modification could reduce the amount of juveniles fish, cuttlefish included, caught by 57% (CEFAS, 2009).

Marine protected areas do not appear to show effective long-term protection for this species due to its mobile and migratory nature (ICES, 2015(b)). It may be effective, however, solely as a protection for the spawning zone, ensuring successful recruitment (ICES, 2015(b)).

No specific management measure has been introduced in the UK to date to maintain and manage commercially important English Channel cuttlefish stock. There is no minimum size limit for shore caught cephalopods and it is a non-quota species in the UK (British Sea Fishing, 2018). There is, however, a minimum conservation reference size in UK waters for the octopus *Octopus vulgaris* of 750g (Marine Management Organisation, 2017) meaning at least one species of cephalopod is currently managed in the UK.

In Spain, there is a minimum landing size of 8 cm for small-scale fisheries and during the months of May to July and fishing must occur above 5 m depth for boats less than 2.5 GRT (RAGG, 2015; cited in Guerra *et al.*, 2016(b)). There is a similar size/weight restriction enforced in Portugal for *Sepia officinalis* (Hastie *et al.*, 2009). *Sepia officinalis* is currently described as 'least concern' on the IUCN red list (IUCN, 2009).

Aquaculture

Sepia officinalis has been successfully cultured in both aquaria and aquaculture. The species is used for biomedical and environmental research and is thought to be the most easily cultured cephalopod species (Forsythe *et al.*, 1994, Domingues *et al.*, 2001, Koueta *et al.*, 2006).

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